

Regenerating mahogany (*Swietenia macrophylla*) from seed in Quintana Roo, Mexico: the effects of sowing method and clearing treatment[☆]

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Abstract

Honduras or bigleaf mahogany (*Swietenia macrophylla* King) is the most commercially important timber species in the Neotropics, but it often does not regenerate successfully after harvesting. Effective methods are needed to sustain or increase mahogany yields by increasing regeneration. This study evaluates the effects of three treatments (slash, fell and burn; slash, fell and leave; and uprooting and pushing away trees using machines) used to open 0.5 ha clearings, plus a control under the forest canopy, and two sowing methods (surface-sown seed and buried seed) on the germination, establishment, survival, and early growth of mahogany. After 10 months, significantly more buried seeds yielded established seedlings (20%) than surface-sown seeds (9%), but there were no significant differences among clearing treatments. Establishment on controls averaged 18%.

The percentage of seedlings that survived from 10 to 49 months varied significantly among treatments, from 53 to 54%, respectively, on the slash and burn and machine-cleared treatments to 16% on the fell and leave treatment and 26% on controls. Both slash and burn and machine-clearing reduced sprouting as compared to the fell and leave treatment, which had abundant sprouting from stumps of other species and the lowest establishment and survival of mahogany. Low survival on controls was probably due to low light levels. Forty-nine months after sowing, an average of 12% of the seeds buried in the slash and burn and machine-cleared treatments were represented by live seedlings, a rate substantially higher than on the fell and leave treatment (3%) and the control (6%). Yield from buried seeds averaged 9% as compared to 4% from surface-sown seeds. Seedling height at 49 months (average = 66 cm) did not differ significantly among the clearing treatments or sowing methods, but on control plots average height of the few surviving seedlings was only 27 cm.

The traditional slash and burn practice used for agricultural clearing seems to be a good way to prepare sites for seeding with mahogany and could be used as a silvicultural technique to facilitate regeneration. Consideration should be given to integrating these systems into forest management to help assure continued production of mahogany.

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1. Introduction

Honduras or bigleaf mahogany (*Swietenia macrophylla* King) is the most commercially important timber species in tropical America (Lamb, 1966; Weaver and Sabido, 1997; Mayhew and Newton, 1998). Unfortunately, mahogany regeneration is

typically unsuccessful after selective harvesting, also referred to as diameter-limit harvesting, which removes from each hectare only a few trees above a specified minimum diameter-limit (Negreros-Castillo, 1991; Snook, 1996; Dickinson and Whigham, 1999).

In Mexico, efforts to regenerate mahogany have focused on planting seedlings in recently logged forests, with little attention given to site preparation. Seedlings planted under the forest canopy and in areas disturbed by selective logging often have low survival and growth, due to competition from existing vegetation (Gerhardt, 1994; Negreros-Castillo and Mize, 2003) and rapid canopy closure (Dickinson and Whigham, 1999; Negreros-Castillo, unpublished data). Effective silvicultural methods are needed to ensure and increase regeneration in logged forests to sustain mahogany and help maintain the value of standing forests as a competitive land use.

Mahogany typically regenerates after major disturbances (natural or human-caused) in essentially even-aged mixed-species stands (Stevenson, 1927; Oliphant, 1928; Wolffsohn, 1961; Lamb, 1966; Wolffsohn, 1967; Snook, 1993, 1996, 1998, 2000, 2002; Gullison et al., 1996). A shade-intolerant species with seed viability of only a few months (Parraguirre-Lezama, 1994; Gómez-Tejera, 1996; Morris et al., 2000), mahogany lacks a seed or seedling bank in the understory (Snook, 1993, 2000; Dickinson and Whigham, 1999). Logging all mahogany trees above a 55 cm diameter-limit depletes seed sources (Negreros-Castillo, 1991; Gullison and Hubbell, 1992; Snook, 1996) and leaves a shady, essentially closed-canopy environment, little affected by the removal of one or a few trees per hectare (Whitman et al., 1997), which is unfavorable for the establishment of mahogany seedlings (Dickinson and Whigham, 1999).

Because mahogany has been found to regenerate naturally after patches of forest are opened by disturbance, several studies have been conducted to evaluate techniques that create similar conditions (Stevenson, 1927; Oliphant, 1928; Wolffsohn, 1961; Lamb, 1966; Negreros-Castillo, 1991; Negreros-Castillo and Mize, 1993; Gerhardt, 1994; Negreros-Castillo and Hall, 1994, 1996; Weaver and Sabido, 1997; Dickinson and Whigham, 1999). Those studies focused on degree of canopy opening, methods to eliminate standing trees, and the results of direct seeding, planting, and natural regeneration under

different levels of light and root competition. The objective of the study presented here was to evaluate mahogany establishment, survival, and growth during the first 4 years after seeding in response to three treatments used to create 0.5 ha clearings and two methods of sowing seeds. While a few studies have evaluated direct seeding, none has been this large in plot size and replication, or compared this many site treatments, nor have they documented results over a multi-year period.

2. Methods

2.1. Study area

The study was conducted in the state of Quintana Roo, Mexico (Fig. 1). The forests of Quintana Roo are part of the Maya forest region, and currently represent the largest contiguous block of tropical forest in Mexico (Toledo and Ordoñez, 1993). Because mahogany timber is one of the most valuable products that forest-owning communities (*ejidos*) of Quintana Roo obtain from their forest reserves (Negreros-Castillo, 1991; Richards, 1991; Kiernan and Freese, 1997; Snook, 1998; Negreros-Castillo et al., 2000a,b), three ejidos and a private landowner allowed us to establish mahogany regeneration experiments in their forests (Fig. 1), located between 88°04' and 88°32'W longitude and 19°06' and 19°43'N latitude.

The forests of central and southern Quintana Roo are seasonal tropical forests, examples of the most important tropical forest type in Central America (Murphy and Lugo, 1986). According to the Köppen classification system, modified by García (1988), the climate of the region is classified as Aw, which is defined as warm and submoist with abundant rains in summer and dry winters. Annual rainfall ranges from 1200 to 1500 mm per year, usually falling between June and October, with a dry season averaging 6 months during which rainfall is less than 100 mm per month. The dry season is most extreme between February and April, when rainfall is less than 45 mm per month (SARH, 2000). Soils are derived from limestone, and the topography is relatively flat (INEGI, 1994). These forests have been subjected for centuries to periodic slash and burn agriculture (Gliessman et al., 1981; Edwards, 1986).

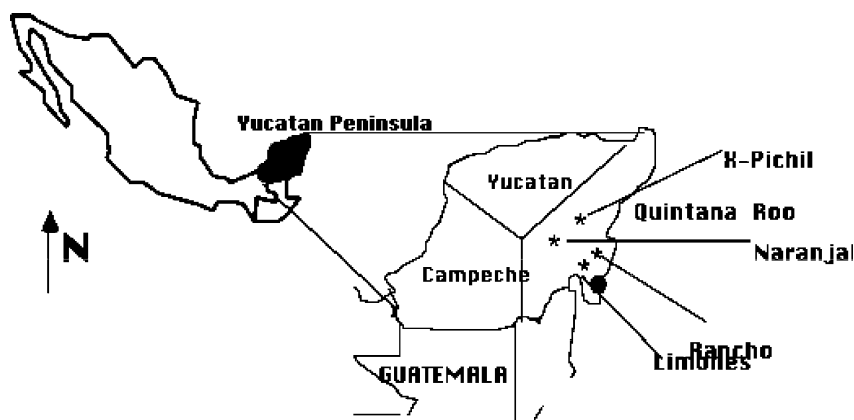


Fig. 1. Location of study sites in Quintana Roo, Mexico.

2.2. Design, measurements, and analysis

This experiment, replicated at four locations within the study area, evaluated the effect of three clearing treatments plus a control, and two sowing methods on the regeneration of mahogany. The forest where experiments were established was at least 50 years old.

2.2.1. Clearing treatments

- (1) *Slash, fell and burn*. This treatment is the traditional practice used to clear agricultural fields in the region (Gliessman et al., 1981) and mimics hurricanes followed by wildfire. All understory vegetation was slashed with machetes, and trees were cut with machetes, axes, or occasionally, chain saws. The vegetation was allowed to dry, then it was burned. At two locations, as the first rains fell, traditional crops (corn, beans, squash and chili peppers) were planted and grown for one or two seasons. On the other two locations no farmers wanted to crop the plots. This treatment will be referred to as slash and burn.
- (2) *Slash, fell and leave*. All understory and overstory vegetation was cut. Some was removed by hand; most was left on site. This treatment will be referred to as fell and leave.
- (3) *Machine-cleared*. Rubber-tired skidders or tracked bulldozers were used to knock over and push vegetation to edges of the plots. On a few clearings, some trees could not be uprooted and were either felled using chainsaws or left

standing. At one location, a farmer planted crops on one of these clearings. This treatment will be referred to as machine-cleared.

- (4) *Control*. Nothing was done to the forest.

2.2.2. Sowing methods

- (1) *Surface-sown seed*. Seeds were laid on the soil surface.
- (2) *Buried seed*. Seeds were buried about 0.5 cm below the soil surface.

At each of the four locations, six $100\text{ m} \times 50\text{ m}$ plots, called clearing plots, were laid out with the long axis oriented east-west (Fig. 2). Each of the three clearing treatments was randomly assigned to two of the six plots, and carried out between April and June 1996. Six $5\text{ m} \times 5\text{ m}$ plots, called seeding plots, were established at intervals along the center of the long axis of each clearing plot (Fig. 2). Each seeding plot contained a 5×5 grid of sowing sites spaced 1 m apart. A stake was put at each site, and around each stake three mahogany seeds were sown in a triangular pattern with about 5 cm between seeds, for a total of 75 seeds per seeding plot. In each clearing plot, three seeding plots were randomly assigned one sowing method, and the other three were sown using the other sowing method. The north and south edges of seeding plots were 22 m from the corresponding edges of the clearing plots, so shading from trees at the edge of the clearing plots, which averaged 20–25 m tall, should not have affected them. The edge of the seeding plots

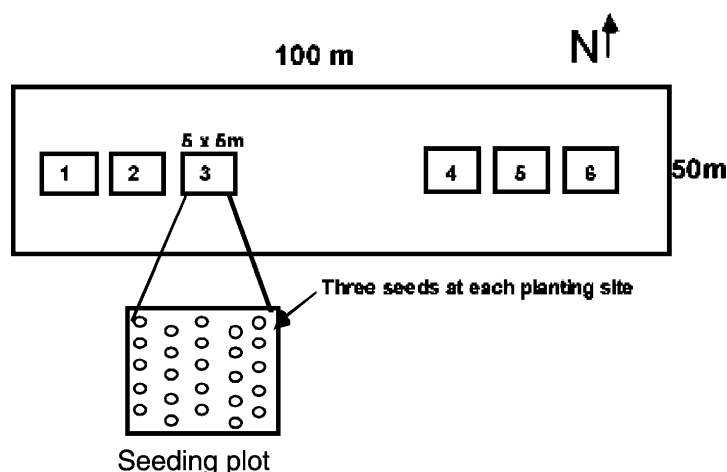


Fig. 2. Layout of experimental plots (not to scale).

nearest the east and west ends of the clearing plots were 5 m from the forest edge, which would have resulted in some shading of these plots, but the effect should have been about the same for all treatments.

Seeds were initially sown on the soil surface between May and June 1996, immediately after clearing. As no seedlings emerged, probably due to seed viability problems (poor storage), direct exposure to heat on the bare soil surface, and/or a lack of rain, the plots were reseeded in April 1997. Although at the time of reseeding new growth and sprouts on all clearing plots had been growing for 1 year and averaged about 1.5 m tall, nothing was done to control new or sprouting vegetation. About 10 m into the undisturbed forest from the edge of most clearing plots a seeding plot was established as a control. Due to time limitations, only 17 control plots were established and randomly assigned to each of the two sowing methods. As a result, there were nine control plots with buried seed and eight with surface-sown seed.

Each sowing site was evaluated 10, 15, 22, 27, 32, and 49 months after reseeding. Measurement dates (February and July), correspond to the end and the beginning of the rainy season, respectively. The height of each live seedling was measured and recorded, and notations were made if the seedling was affected by the shootborer (*Hypsipyla grandella*) or by leaf-cutter ants (*Atta* sp.), or browsed by other animals. During the first three measurements, the number of simple leaves or leaflets of compound leaves on each

seedling was noted. Any volunteer mahogany seedlings were removed from the seeding plots.

Although the study was not designed to evaluate germination, data on germination were taken during the 5 months following seeding. The total number of seeds that had germinated on each seeding plot was recorded every 15–20 days. Also, seed predation was recorded about every 2 weeks for the first 5 months at two locations by visually evaluating each seed, whether surface-sown or buried, at five sowing sites in each seeding plot. Only five sites were evaluated because of the potential impact of evaluating the buried seed. In a third location, the number of seedlings that died during the first 7 months after seeding was recorded about every 2 weeks for all seeding plots. Seed predation and the number of seedlings that died were evaluated at a subset of the locations due to limited funds.

Data were analyzed using analysis of variance (ANOVA). When data from two or more locations were analyzed, average responses were calculated for the six combinations of clearing treatments (the controls were not included) and sowing methods at each location. Averages were analyzed as a replicated complete factorial design with locations as blocks and clearing treatments and seeding methods as the two factors. When data from one location were analyzed, average responses were calculated for both sowing methods in each clearing plot. The averages were analyzed as a completely randomized split plot design with clearing treatments as whole plots and

seeding methods as subplots. As the control plots were not laid out like the other plots, they could not be analyzed with the other treatments, but they were analyzed with ANOVA as a simple blocked design with locations as blocks and seeding methods as treatments, using average responses for buried and surface-sown seeds at each location. All analyses were carried out using SAS (1990).

3. Results

The results are presented for three time periods: initial germination; establishment, which we consider to be at 10 months after seeding; and at 49 months, which is the time of the last measurement.

3.1. Germination

The cumulative percentage of seeds that germinated during the first 5 months after seeding did not differ among the three clearing treatments (average = 13%) ($P = 0.25$), but buried seeds had a much higher germination rate (20%) than surface-sown seeds (6%) ($P < 0.001$, S.E. = 1.4%). ANOVA of the controls revealed the same pattern: germination of buried seeds (34%) was higher than that of surface-sown seeds (15%) ($P = 0.057$, S.E. = 4%).

3.2. Seed predation

In the two locations monitored, an average of 20% seeds planted in each seeding plot was lost to predation during the first 5 months. There were no significant differences among the three clearing treatments ($P = 0.42$) or between the sowing methods ($P = 1.0$). Losses in the controls for the two locations averaged 16 and 28% of seeds for buried and surface seeding, respectively.

3.3. Seedling mortality after germination

The data on seed germination and seedling mortality from a third location were combined to determine the percentage of germinated seeds that died. On average, 24% of the seeds that germinated died during the first 6 months. The total number of germinated seeds that died did not vary among the three clearing

treatments ($P = 0.56$) or between seeding methods ($P = 0.77$). The controls averaged 27 and 23% dead seedlings for buried and surface seeding, respectively.

3.4. Seedling establishment at 10 months

Ten months after seeding, the rate of establishment of seedlings from buried seeds (20%) was significantly greater than from surface-sown seeds (9%) ($P < 0.001$, S.E. = 1), but did not differ significantly among clearing treatments ($P = 0.25$, S.E. = 2). For the controls, rates of establishment were similar to the clearing treatments (Table 1), but the difference between buried and surface-sown seeds was not statistically significant ($P = 0.11$, S.E. = 4). Among all clearing treatments and controls, no seedlings established on 58% of the sowing sites for buried seeds compared to 79% of the surface-sown sites (Table 2).

Table 1
Percentage of seeds represented by a live seedling 10 months after sowing and average height of seedlings by clearing treatment and seeding method (standard error in parentheses)

| Treatment | Percentage seeds represented by a live seedling | | Height (cm) | |
|-----------------|---|-----------------------|-------------------|-----------------------|
| | Buried | Surface | Buried | Surface |
| Slash and burn | 22 ^{a,b} | 11 ^{a,b} (1) | 27 ^{a,b} | 25 ^{a,b} (1) |
| Machine-cleared | 22 ^{a,b} | 7 ^{a,b} (1) | 29 ^{a,b} | 26 ^{a,b} (1) |
| Fell and leave | 16 ^{a,b} | 8 ^{a,b} (1) | 27 ^{a,b} | 25 ^{a,b} (1) |
| Control | 24 ^a | 12 ^a (3) | 19 ^a | 20 ^a (1) |

^a Differences due to seeding treatment not significant ($P > 0.05$).

^b Differences due to clearing treatment not significant ($P > 0.05$).

Table 2
Frequency of established seedlings per sowing site 10 months after sowing three seeds per site, by treatment and sowing method

| Treatment | Percentage of sites with | | | |
|-------------------|--------------------------|------------|-------------|-------------|
| | 0 seedlings | 1 seedling | 2 seedlings | 3 seedlings |
| Slash and burn | 64 | 24 | 10 | 2 |
| Machine-cleared | 69 | 21 | 7 | 3 |
| Fell and leave | 73 | 18 | 7 | 2 |
| Control | 64 | 20 | 15 | 2 |
| All combined | 68 | 21 | 9 | 2 |
| Buried seed | 58 | 26 | 12 | 3 |
| Surface-sown seed | 79 | 15 | 5 | 1 |

The average height of seedlings 10 months after seeding (average = 27 cm) did not vary significantly among the three clearing treatments ($P = 0.20$, S.E. = 1), but seedlings on controls averaged only 19 cm (Table 1). Sowing method did not affect seedling heights on controls ($P = 0.46$, S.E. = 1), and differences were minimal on cleared plots ($P = 0.063$, S.E. = 1), with seedlings from buried seeds averaging 28 cm versus 26 cm for seedlings from surface-sown seed. Ten months after seeding, none of the 1808 seedlings had been attacked by *H. grandella*, and only 2% of the seedlings had been browsed. About 6% of the seedlings showed evidence of herbivory by leafcutter (*Atta* sp.) ants. ANOVA indicated that ant damage was not significantly different among clearing treatments or between seeding methods ($P > 0.2$).

3.5. Number of leaves

ANOVAs of the number of leaves or leaflets per seedling 10, 15, and 22 months after planting showed that seedlings derived from buried seeds produced more leaves than those from surface-sown seeds, by 33, 31, and 21%, respectively ($P = 0.003$, $P < 0.001$, $P = 0.097$, respectively). The number of leaves at these three measurement periods also differed among clearing treatments ($P = 0.003$, $P < 0.001$, and $P < 0.001$, respectively) with seedlings on machine-cleared and slash and burn plots having about the same number of leaves, while seedlings on fell and leave plots had significantly fewer. Seedlings on the clearing treatments averaged 8, 12, and 14 leaves, respectively, for the first three measurement periods, while seedlings in control plots averaged 5, 5, and 6 leaves over the same periods. On controls, differences between seeding methods in the number of leaves per seedling were not significant ($P > 0.60$ for all three measurement periods).

3.6. Survival over time

After an initial large drop in numbers of surviving seedlings between 10 and 15 months after sowing (Fig. 3), the number of surviving seedlings decreased in a linear fashion. Considering only the seedlings alive after 10 months, rates of survival at the last measurement, 49 months after seeding, varied significantly among clearing treatments ($P < 0.001$).

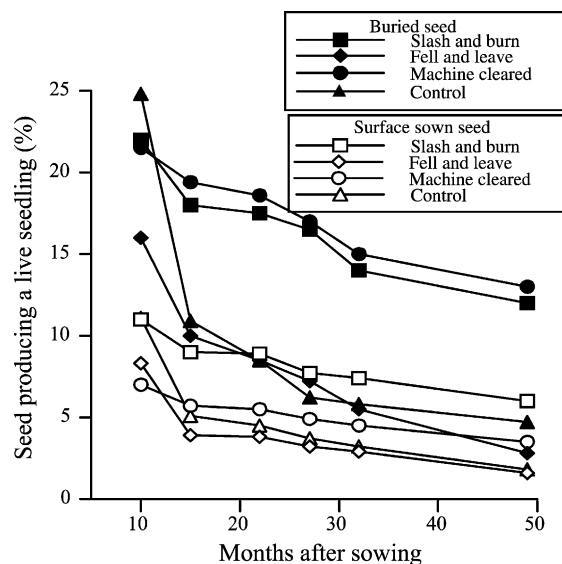


Fig. 3. Average percentage of seeds yielding live seedlings after 49 months for eight combinations of clearing treatment and sowing method.

Survival of established seedlings 39 months later ranged from 53 to 54%, respectively, on slash and burn and machine-cleared plots to 16% on felled plots and 26% on controls (Table 3). Differences due to seeding method were not significant ($P = 0.51$ in cleared treatments, $P = 0.60$ on controls).

The percentage of sown seeds that yielded a live seedling at 49 months differed between sowing methods ($P = 0.005$, S.E. = 1) and among clearing treatments ($P = 0.008$, S.E. = 1) (Table 4). Yields (percentage of sown seed that produced a live seedling) from buried seeds ranged from 12% on slash and

Table 3

Percentage of seedlings established at 10 months that were alive at 49 months^a (standard error in parentheses)

| Treatment | Established seedlings surviving (%) | |
|-----------------|-------------------------------------|---------------------|
| | Buried | Surface |
| Slash and burn | 53 ^b | 64 ^b (4) |
| Machine-cleared | 55 ^b | 52 ^b (4) |
| Fell and leave | 15 ^b | 11 ^b (4) |
| Control | 10 ^b | 9 ^b (3) |

^a Percentage = (# alive after 49 months/# alive after 10 months) × 100.

^b Differences due to seeding method are not significant.

Table 4

Percentage of seeds yielding a live seedling 49 months after sowing and average height of seedlings by clearing treatment (standard error in parentheses)

| Treatment | Percentage seeds yielding a live seedling | | Height (cm) | |
|-----------------|---|--------------------|-------------------|------------------------|
| | Buried | Surface | Buried | Surface |
| Slash and burn | 11 | 6 (2) | 72 ^{a,b} | 61 ^{a,b} (13) |
| Machine-cleared | 13 | 3 (2) | 76 ^{a,b} | 72 ^{a,b} (13) |
| Fell and leave | 3 | 1 (2) | 57 ^{a,b} | 48 ^{a,b} (13) |
| Control | 6 ^a | 2 ^a (2) | 27 ^a | 27 ^a (1) |

^a Difference due to seeding method not significant ($P > 0.05$).

^b Differences due to clearing treatment not significant ($P > 0.05$).

burn and machine-cleared plots to 3% on fell and leave treatments. For surface-sown seeds, yields ranged from 6% on slash and burn to 1% on fell and leave treatments. On controls, the difference in percentage yield between seeding methods was not significant ($P = 0.24$, S.E. = 2). At 49 months, there were no live seedlings on 78% of the sites where seeds had been buried and 91% of the sites where seeds had been placed on the soil surface. On the fell and leave treatment and controls, only 6% of the sites, on average, had seedlings 49 months later (Table 5).

3.7. Height over time

For the first three measurement periods, height growth was almost identical on the three clearing treatments (Fig. 4). After that, the growth rate of the seedlings on fell and leave plots decreased compared to growth rates on the other two clearing treat-

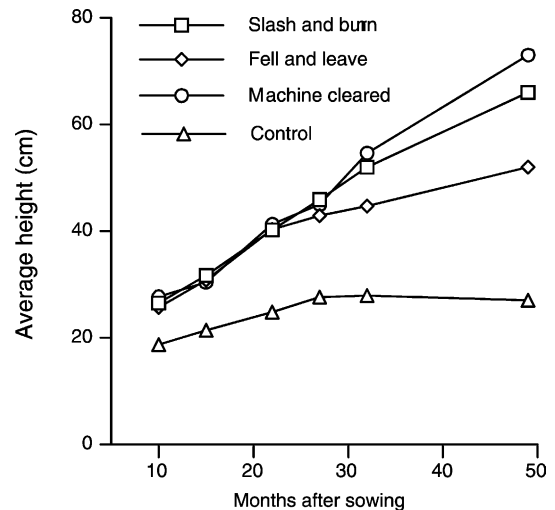


Fig. 4. Average height of seedlings to 49 months by clearing treatment. Standard error approximately 1.3 cm for controls and approximately 4 cm for other treatments.

ments. The control seedlings consistently grew more slowly than those on the other treatments, and the few survivors appeared to have almost stopped growing. Neither clearing treatment nor seeding method was found to have had a significant effect on average seedling height at 49 months ($P = 0.28$; $P = 0.49$, respectively). Average height on the controls (27 cm) was 41% of the average on the three clearing treatments (66 cm) (Table 4 and Fig. 4).

3.8. Seedling damage

At 49 months, 12 of the 744 surviving seedlings had been attacked by *H. grandella*, and 31 showed ant damage. Relative frequency of ant and *H. grandella* attack were almost identical for both seeding methods. The slash and burn seedlings had the highest rate of *H. grandella* attack (4%), while the other three treatments averaged about 0.5% attacked. The control seedlings had the fewest ant attacks, 0 out of 31, while the other three treatments had similar attack rates of about 5%.

3.9. Block effects and interactions

Differences among the four locations where the plots were established (blocks) were generally not significant ($P > 0.10$). Average height after 10 months

Table 5

Frequency of established seedlings per sowing site 49 months after sowing 3 seeds/site

| Treatment | Percentage of sites with | | | |
|-------------------|--------------------------|------------|-------------|-------------|
| | 0 seedlings | 1 seedling | 2 seedlings | 3 seedlings |
| Slash and burn | 78 | 17 | 4 | 1 |
| Machine-cleared | 79 | 17 | 3 | 1 |
| Fell and leave | 94 | 5 | 1 | 0 |
| Control | 93 | 6 | 2 | 0 |
| Buried seed | 78 | 17 | 4 | 1 |
| Surface-sown seed | 91 | 8 | 1 | 0 |
| All combined | 85 | 12 | 3 | 0 |

varied among locations ($P = 0.034$), but the difference between the tallest (Rancho) and the shortest (Naranjal) was only 5 cm, in relation to an overall average of 27 cm. Total number of leaves varied among locations for the first two measurements ($P < 0.05$) but not the third ($P > 0.35$). The only significant interaction between seeding method and clearing treatment was for percentage of seeds sown represented by a live seedling after 49 months ($P = 0.053$). The difference between seedling yields from buried and surface-sown seed on the fell and leave plots was much smaller than the differences for the other two treatments (Fig. 3), probably reflecting the relatively low survival of seedlings on the fell and leave clearings.

4. Discussion

In plots on clearings, burying mahogany seeds was clearly better than sowing them on the soil surface, yielding double the number of established seedlings after 10 months. Interestingly, seed predation and seedling mortality were about the same for both sowing methods. Thus, the greater success of buried seeds seems to be primarily due to higher germination, which, in plots on clearings, was about three times greater than that of surface-sown seeds. Surface-sown seeds in clearings faced desiccating heat, while buried seeds were protected from both heat and desiccation.

Although burying seeds is preferable, only 21% of the sites where three seeds had been buried on slash and burn or machine-made clearings had one or more seedlings 4 years later (Table 5), yielding a density of about 5 seedlings per 25 m² plot. This density is probably lower than it would be if seeds were sown the same year clearings were opened, before vegetation began to regrow. Sowing the same year that clearings are created and sowing more seeds per site would be expected to increase the percentage of sites with at least one mahogany seedling. Careful selection of sowing sites might also yield better results, as mahogany may be sensitive to microsite (Negreros-Castillo, unpublished data).

During the first three measurements, the number of leaves per seedling was influenced by clearing treatment and sowing method. The machine-cleared and slash and burn plots had the tallest seedlings with the

most leaves. Although the two sowing methods did not affect height growth in clearing treatments, seedlings from buried seeds had more leaves than seedlings from surface-sown seeds. Burying seeds might allow faster root growth than surface seeding, allowing extra energy from the seeds to be used for leaf development. Despite the differences in leaf numbers at the third measurement, by the last measurement seedling height was not significantly affected by seeding method or by clearing treatment.

The control plots under the canopy of the 20 m tall forest had low light levels, which resulted in 94% mortality over 49 months, and substantially reduced seedling growth (Table 4). Clearing treatments changed two site characteristics, light level and competing vegetation, as compared to the undisturbed forest. Because all clearing plots were the same size (0.5 ha), light levels on all the clearings were expected to be the same, and considerably higher than under a forest canopy. Differences among the three clearing treatments were primarily due to differences in the density, structure, and composition of the vegetation that became established after clearing. The slash and burn and machine-cleared treatments yielded similar densities of mahogany seedlings 49 months later (21% of sites with one or more live seedlings), more than triple the yield on the fell and leave treatment and the controls. Both burning and uprooting vegetation impede sprouting (Rewald, 1989; Snook, 1993), while felling results in vigorous resprouting from stumps and roots (Negreros-Castillo and Hall, 2000; Dickinson et al., 2000). As a result, mahogany seedlings on the fell and leave plots were subjected to much greater competition compared to the other two treatments, which impeded both survival and growth. Despite similar levels of establishment and growth, the slash and burn treatment is preferable to machine-clearing in this region, because it has less impact on the soil, it is much less expensive, and it is an integral part of the farming system used for centuries and well understood by the thousands of local farmers who are the owners of hundreds of thousands of hectares of forest in Quintana Roo.

Aside from this study, we are evaluating the growth of seedlings planted on the clearing treatment plots (Snook and Negreros-Castillo, in press), and other researchers are following the progress of the vegetation that became established naturally on the clearing

treatments. We plan to take measurements on the plots for another 15 years.

5. Implications for mahogany silviculture

This study confirmed previous observations (Lamb, 1966) that mahogany seeds germinate successfully in the shade (Morris et al., 2000) but that the resulting seedlings do not survive for long under a canopy because of low light levels. Although clearings have high initial light levels, clearing treatments need to reduce competition from regrowing or newly established vegetation if mahogany seedlings are to survive. The machine-cleared and slash and burn treatments in this study removed the overstory and reduced both initial and subsequent competition, resulting in much higher survival of mahogany seedlings than both the fell and leave and the control treatments.

Compared to sowing seeds, planting seedlings has the advantage that they are at least 20 cm tall and able to compete with regrowing vegetation. Three months after they were seeded, 4-month-old (20 cm tall) mahogany seedlings were planted on the treatment plots used in this study. Seedling survival was 50% 46 months after planting, while the yield of live seedlings from buried seeds was 12% of sown seeds and 21% of sown sites after 49 months. During this period, planted, uncleaned seedlings on machine-clearings had reached heights averaging 146 cm (Snook and Negreros-Castillo, in press), compared to a maximum height from sown seed of 74 cm (on machine-cleared plots). A drawback of planting seedlings, however, is their weight and size, which makes it difficult to transport them to sites with limited access. Production, transportation, and planting costs are also high, and sometimes seedlings are poorly planted, undermining their survival and growth (Negreros-Castillo and Mize, 2003).

Given that 1 kg of mahogany seeds contains about 2000 seeds (Gómez-Tejera, 1996; Whitmore and Hinojosa, 1977), a person could carry enough seeds to sow several thousand sites. Although it takes slightly longer to bury seeds than to toss them on the surface, it is not only more efficient, but, assuming high seed viability, permits better control of the distribution of seedlings. The time of sowing can affect seed viability, predation, and exposure to direct sun.

Sowing shortly after the beginning of the rainy season should increase both germination and survival (Morris et al., 2000).

Slash and burn agriculture, which mimics hurricanes followed by wildfires, is one of the clearing treatments that yielded the best results in this study. It has been a common disturbance in the region for centuries and has favored the establishment of mixed-species stands rich in mahogany (Stevenson, 1927; Oliphant, 1928; Wolffsohn, 1961, 1967; Lamb, 1966; Negreros-Castillo, 1991; Snook, 1993, 1996, 1998, 2000, 2002). In Quintana Roo, and perhaps throughout the entire Maya forest region (Belize, Guatemala and Mexico), an important opportunity exists to use slash and burn as a silvicultural practice to regenerate mahogany. Slash and burn agriculture is practiced annually by thousands of farmers, many of whom are also responsible for forest management.

In conclusion, burying mahogany seed in recently established slash and burn fields could help sustain or increase the mahogany resource in the community forests in this region. Mahogany seeds could be sown along with agricultural crops in slash and burn fields the year they are cleared. During the first year or two, vegetation competing with mahogany seedlings could be controlled during normal crop weeding. When fields are abandoned, in the second or third year, mahogany seedlings should be well-established and able to compete with the vegetation that recolonizes a site when it is abandoned. It is noteworthy that between the 1920s and the 1960s the Belize Forest Department used direct (buried) seeding to regenerate mahogany in this way, under the taungya system, whereby they arranged for farmers to sow mahogany seeds at the time they sowed their maize in slash and burn fields on government land (Oliphant, 1928; Lamb, 1947 in Mayhew and Newton, 1998, p. 55; Lamb, 1966; Ennion, 2002). Direct seeding is still used to regenerate mahogany in Fiji (SRD, 1995 in Mayhew and Newton, 1998, p. 56). The mixture of species that currently becomes established naturally on abandoned slash and burn fields in the region may limit the attack of the *H. grandella* shootborer, widely considered a significant impediment to the growth, form and survival of mahogany. A number of studies have observed, as occurred in this experiment, that *H. grandella* attack is reduced when mahogany grows in mixed-species stands (Lamb, 1966; Snook, 1993;

Mayhew and Newton, 1998, pp. 134–135; Joao et al., 1996; Snook and Negreros-Castillo, in press; Negreros-Castillo, unpublished data).

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References

- Dickinson, M.B., Whigham, D.F., 1999. Regeneration of mahogany in the Yucatan. *Int. For. Rev.* 1 (1), 35–39.
- Dickinson, M.B., Whigham, D.F., Herman, S.M., 2000. Tree regeneration in felling and natural tree fall disturbances in a semideciduous tropical forest in Mexico. *For. Ecol. Manage.* 134, 137–151.
- Edwards, C.R., 1986. The human impact on the forest in Quintana Roo, Mexico. *J. For. History* 30, 120–127.
- Ennion, R.C., 2002. Evaluation of four taungya permanent big-leaf mahogany plots, aged 36 to 38 years, in Belize. In: Lugo, A., Figueroa, J., Alayón, M. (Eds.), *Big-Leaf Mahogany Ecology, Genetics and Management, Ecological Studies*, vol. 159, Springer, Berlin, Chapter 19, pp. 362–374.
- García, E., 1988. Modificaciones al sistema de clasificación climática de Köppen (para adaptarlo a las condiciones de la

- Republica Mexicana). Geography Institute, Autonomous University of Mexico, Mexico, 252 pp.
- Gerhardt, K., 1994. Seedling development of four tree species in secondary tropical dry forest in Guanacaste, Costa Rica, vol. 39. Comprehensive Summaries of Uppsala Dissertations. Faculty of Science and Technology, 43 pp.
- Gliessman, S.R., Garcia, R.E., Amador, M.A., 1981. The ecological basis for the application of traditional agricultural technology in the management of tropical agro-ecosystems. *Agro-Ecosystem* 7, 173–185.
- Gómez-Tejera, J., 1996. Deterioro de la viabilidad de la semilla de *Swietenia macrophylla* King bajo distintas condiciones de almacenamiento. M.S. Thesis. Postgraduate College, Montecillo, MX, 88 pp.
- Gullison, R.E., Hubbell, S., 1992. Regeneración natural de la maha (*Swietenia macrophylla*) en el bosque Chimanes, Bolivia. *Ecol. Bolivia* 19, 43–56.
- Gullison, R.E., Panfil, S.N., Strouse, J.J., Hubbell, S.P., 1996. Ecology and management of mahogany (*Swietenia macrophylla* King) in the chimanes forest, Beni, Bolivia. *Bot. J. Linn. Soc.* 122, 9–34.
- INEGI, 1994. Anuario estadístico del estado de Quintana Roo. INEGI and the government of Quintana Roo, 244 pp.
- Joao, M.C.S., De Sousa, S.G.A., Wandelli, E., Perin, R., Arcoverde, Fernandes, E.C.M., 1996. Performance of mahogany (*Swietenia macrophylla* King) in agroforestry systems in the western Amazon region in Brazil. In: Proceedings of the International Conference on Big-Leaf Mahogany: Genetic Resources, Ecology and Management, San Juan, Puerto Rico.
- Kiernan, M.J., Freese, C.H., 1997. Mexico's Plan Piloto Forestal: the search for balance between socioeconomic and ecological sustainability. In: Freese, C.H. (Ed.), *Harvesting Wild Species: Implications for Biodiversity Conservation*. Johns Hopkins University Press, Baltimore, MD, Chapter 3, 703 pp.
- Lamb, F.B., 1966. Mahogany of Tropical America: its Ecology and Management. University of Michigan Press, Ann Arbor.
- Mayhew, J.E., Newton, A.C., 1998. The Silviculture of Mahogany. Institute of Ecology and Research Management, University of Edinburgh, UK. CAB International, Wallingford, 226 pp.
- Morris, M., Negreros-Castillo, P., Mize, C.W., 2000. Sowing date, shade, and irrigation affect big-leaf mahogany (*Swietenia macrophylla* King). *For. Ecol. Manage.* 132, 173–181.
- Murphy, P.G., Lugo, A.E., 1986. Ecology of a tropical dry forest. *Ann. Rev. Ecol. Syst.* 17, 67–88.
- Negreros-Castillo, P., 1991. Ecology and management of mahogany (*Swietenia macrophylla* King) regeneration in Quintana Roo, Mexico. Ph.D. Dissertation. Iowa State University, Ames, IA, 125 pp.
- Negreros-Castillo, P., Hall, R.B., 1994. Four methods for partial overstory removal in tropical forests in Mexico. *J. Environ. Manage.* 41, 237–243.
- Negreros-Castillo, P., Hall, R.B., 1996. First-year results of partial overstory removal and direct seeding of mahogany (*Swietenia macrophylla*) in Quintana Roo, Mexico. *J. Sust. For.* 3 (23), 65–76.
- Negreros-Castillo, P., Hall, R.B., 2000. Sprouting capability of 17 tropical tree species after overstory removal in Quintana Roo, Mexico. *J. For. Ecol. Manage.* 126, 399–403.
- Negreros-Castillo, P., Mize, C.W., 1993. Effects of partial overstory removal on natural regeneration of a tropical forest in Quintana Roo, Mexico. *For. Ecol. Manage.* 58, 259–272.
- Negreros-Castillo, P., Mize, C., 2003. Enrichment planting of *Swietenia macrophylla* (big leaf mahogany) and *Cedrela odorata* (Spanish cedar) Quintana Roo, Mexico. In: Lugo, A.E., Figueroa Colon, J.C., Alayon, M. (Eds.), *Big-Leaf Mahogany Ecology, Genetics and Management*, Ecological Studies, vol. 159. Springer-Verlag, New York.
- Negreros-Castillo, P., González Nuñez, J.C., Merino Pérez, L., 2000a. Evaluación de la sustentabilidad del sistema de manejo forestal de la organización de ejidos productores forestales de la zona Maya de Quintana Roo. In: Masera, O., López-Ridaura, S. (Eds.), *Sustentabilidad y sistemas campesinos: cinco experiencias de evaluación en el México rural*. Mundi-prensa México, S.A. de C. V. México, DF, pp. 83–141.
- Negreros-Castillo, P., Merino, L., Gonzalez, J.C., 2000b. Community forestry and sustainability: Maya Forest community organization case study. Prepared for delivery at the 1998 meeting of the Latin American Studies Association, the Palmer House Hilton Hotel, Chicago, IL, September 24–26, 1998, 15 pp.
- Oliphant, J.N., 1928. The cultivation of mahogany in British Honduras. In: *Third British Empire Forestry Conference*. Government Printer, Belize City, Belize, pp. 517–524.
- Parraguirre-Lezama, C., 1994. Germinación de semillas de especies de vegetación primaria y secundaria (estudio comparativo). Undergraduate Thesis. Autonomous University of Chapingo, Chapingo, MX, 89 pp.
- Rewald, M., 1989. Stump sprouts in the milpa cycle and their role in forest regeneration. Masters Thesis. York University, Canada, 169 pp.
- Richards, E.M., 1991. The forest ejidos of south-east Mexico: a case study of community based sustained yield management. *Commonwealth For. Rev.* 70 (4), 290–311.
- SARH (Secretaria de Agricultura y Recursos Hidraulicos), 2000. Subdireccion de Hidrologia, Departamento de Calculo Hidrometrico y Climatologico, Oficina de Calculo Climaticologico, Chetumal, Quintana Roo. Climatic records from meteorological stations at Xpichil, Vallehermoso, Andres Quintana Roo, Limones and INIA. Unpublished.
- SAS Institute, 1990. SAS Procedure Guide, Version 6, 3rd ed. SAS Institute, Inc., Cary, NC, 705 pp.
- Snook, L.K., 1993. Stand dynamics of mahogany (*Swietenia macrophylla* King) and associated species after fire and hurricane in the tropical forests of the Yucatan Peninsula, Mexico. Doctoral Dissertation. Yale School of Forestry and Environmental Studies, Yale University, New Haven, CT, 254 pp.
- Snook, L.K., 1996. Catastrophic disturbance, logging, and the ecology of mahogany: grounds for listing a major tropical timber species in CITES. *Bot. J. Linn. Soc.* 122 (1), 35–46.
- Snook, L.K., 1998. Sustaining harvests of mahogany (*Swietenia macrophylla* King) from Mexico's Yucatán Forests: past, present and future. In: Primack, R., Bray, D., Galletti, H., Ponciano, I. (Eds.), *Timber, Tourists, and Temples: Conservation and Development in the Maya Forest of Belize, Guatemala, and Mexico*. Island Press, Washington, DC, pp. 61–80.

- Snook, L.K., 2000. Regeneración y crecimiento de la caoba en las selvas naturales de Quintana Roo, vol. 86. Ciencia Forestal en México, México, DF.
- Snook, L.K., 2002. Regeneration, growth and sustainability of mahogany (*Swietenia macrophylla* King) in Mexico's Yucatan forests. In: Lugo, A., Figueroa, J., Alayón, M. (Eds.), Big-Leaf Mahogany Ecology, Genetics and Management, Ecological Studies, vol. 159, Springer, Berlin, pp. 169–192.
- Snook, L.K., Negreros-Castillo, P., 2003. Regenerating mahogany (*Swietenia macrophylla* King) on clearings in Mexico's Maya Forest: the effects of clearing treatment and cleaning on seedling survival and growth. Forest Ecology and Management.
- Stevenson, N.S., 1927. Silvicultural treatment of mahogany forests in British Honduras. Empire Forestry J. 6, 219–227.
- Toledo, V.M., Ordoñez, M.de.J., 1993. The biodiversity scenario of Mexico: a review of terrestrial habitats. In: Ramamorthy, T.P., Bye, R., Lot, A. (Eds.), The Biological Diversity of Mexico: Origins and Distribution. Oxford University Press, New York, pp. 757–777.
- Weaver, P.L., Sabido, O.A., 1997. Mahogany in Belize: a historical perspective. USDA For. Serv. So. Res. Sta. Gen. Tech. Rep. IITF-2, 31 pp.
- Whitman, A., Brokaw, N.V.L., Hagan, J.M., 1997. Forest damage caused by selection logging of mahogany (*Swietenia macrophylla*) in northern Belize. For. Ecol. Manage. 92, 87–96.
- Whitmore, J.L., Hinojosa, G., 1977. Mahogany (*Swietenia*) hybrids. USFS Research Paper IITF-23, 8 pp.
- Wolffsohn, A.L.A., 1961. An experiment concerning mahogany germination. Empire For. Rev. 40 (1), 71–72.
- Wolffsohn, A.L.A., 1967. Post-hurricane forest fires in British Honduras. Commonwealth For. Rev. 46 (3), 233–238.