SEED DISPERSAL OF BIG-LEAF MAHOGANY (*SWIETENIA MACROPHYLLA*) AND ITS ROLE IN NATURAL FOREST MANAGEMENT IN THE YUCATÁN PENINSULA, MEXICO

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CÁMARA-CABRALES L & KELTY MJ. 2009. Seed dispersal of big-leaf mahogany (*Swietenia macrophylla*) and its role in natural forest management in the Yucatán Peninsula, Mexico. As part of efforts to design appropriate silvicultural methods for sustainable forest management of big-leaf mahogany (*Swietenia macrophylla*: Meliaceae) in natural mixed forests of Quintana Roo, Mexico, a study of seed dispersal of 11 mahogany seed trees was undertaken. Both small (50–74 cm diameter at breast height, dbh) and large (75–100 cm dbh) seed trees showed seed distributions that were skewed to the west, generally matching the prevailing easterly trade winds. Total mean seed production of trees in the smaller size class was one-half of that of the large trees. Maximum seed dispersal distance was 50 m in the westerly directions (NW–W–SW) and only 20–30 m in other directions. Total seed dispersal areas were 0.4 and 0.5 ha for the small and large trees respectively. These results are important for designing seed tree or shelterwood regeneration methods for mahogany; they provide guidelines for creating the size and spatial layout of an overstorey felling and site preparation treatment that would match the dispersal area.

Keywords: Seed-tree method, tropical silviculture, wind dispersal, polycyclic harvest, community forest, tree seed shadow, high value Meliaceae

CÁMARA-CABRALES L & KELTY MJ. 2009. Penyebaran biji benih mahogani berdaun besar (*Swietenia macrophylla*) dan peranannya dalam pengurusan hutan asli di Semenanjung Yucatán, Mexico. Satu kajian yang melibatkan penyebaran biji benih 11 pokok biji benih mahogani dijalankan sebagai sebahagian daripada usaha untuk membangunkan kaedah silvikultur yang sesuai bagi pengurusan mampan hutan mahogani berdaun besar (*Swietenia macrophylla*: Meliaceae) di hutan campur semula jadi di Quintana Roo, Mexico. Pokok biji benih kecil (50–74 cm diameter aras dada, dbh) dan besar (75–100 dbh) menunjukkan penyebaran biji benih yang terpencong ke barat dan pada umumnya selari dengan angin pasat timuran. Min jumlah penghasilan biji benih pokok yang lebih kecil adalah separuh berbanding pokok besar. Jarak maksimum penyebaran biji benih ialah 50 m di arah barat (barat laut–barat–barat daya) dan cuma 20–30 m di arah lain. Jumlah luas penyebaran biji benih adalah masing-masing 0.4 ha dan 0.5 ha untuk pokok kecil dan besar. Keputusan ini penting dalam usaha membangunkan kaedah pertumbuhan semula bagi pokok biji benih atau sistem naung bagi mahogani. Ini kerana keputusan kajian ini menyediakan garis panduan untuk menetapkan saiz serta reka letak ruang bagi penebangan tingkat atas serta rawatan persediaan tapak yang sama luasnya dengan kawasan penyebaran.

INTRODUCTION

Prior to the 18th century, big-leaf mahogany (*Swietenia macrophylla*: Meliaceae) had a nearly continuous distribution from southern Mexico through Central America to eastern Brazil (Lamb 1966, Patiño-Valera 1997). Mahogany has long been the most valuable timber species in tropical America, with substantial harvesting for international trade having begun in 1750. Since that time, selective logging and deforestation for agricultural development has reduced the area of forest containing mahogany (Lamb 1966). This species is now rare or absent throughout much of its original distribution (Patiño-Valera 1997).

The state of Quintana Roo in the Yucatán Peninsula (Figure 1) is one of the few areas in Mexico where mahogany timber continues to be harvested from extensive natural forests. Much of the forest land in central Quintana Roo is under the control of local communities (*ejidos*) which have a communal form of land tenure that was

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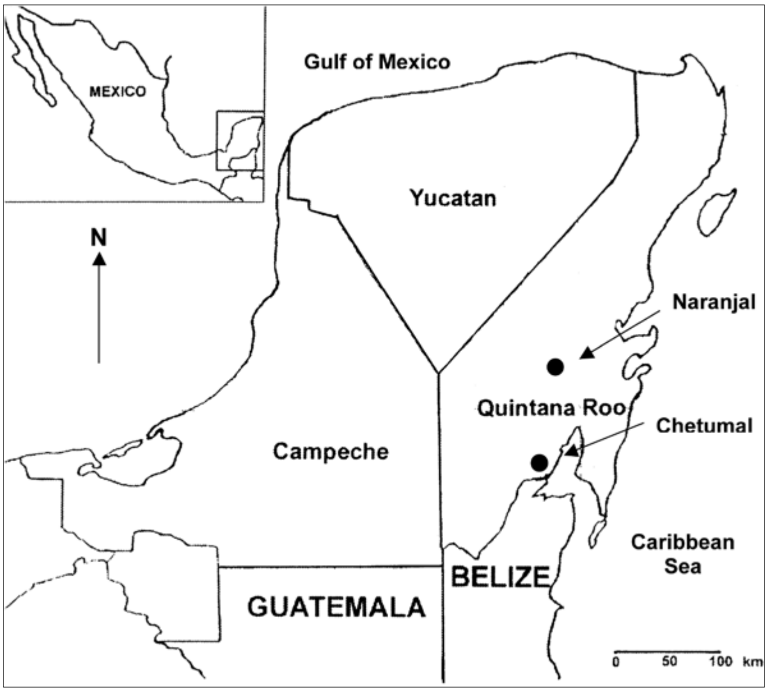

Figure 1 Map of the Yucatán Peninsula showing the forest study site at Naranjal and the location of the city of Chetumal where weather data were taken

established in the region in the early 20th century. Sustainable timber production has become an important economic objective of the *ejidos,* particularly in the Mayan region. The communities have had control of the management of their forests since the mid-1980s, within the regulatory framework of the Mexican federal government (Bray & Klepeis 2003). *Ejidos* throughout Mexico have attracted considerable attention as models for community forest enterprises that seek to provide social and ecological benefits through the management of commercial timber production (Bray *et al.* 2003).

Forest management plans in the 1980s were initially focused on conducting inventories to determine sustainable yield levels (Vester & Navarro-Martínez 2005). Harvest plans prescribed the use of polycyclic harvesting with 25-year cutting cycles; the harvests targeted mahogany trees ≥ 55 cm in diameter at breast height (dbh; 1.3 m height). More recently, other species that have lower timber value have been harvested to a minimum dbh of 35 cm. The tree volumes removed in the first and second cutting cycles were to be balanced by growth of trees < 55 cm dbh, and studies of diameter growth rates of mahogany were established to provide data for regulating harvest levels (e.g. Snook 2003, Shono & Snook 2006). However, long-term sustainability depends upon the establishment and growth of new seedlings. Thus, an additional management requirement was to plant seedlings of mahogany and Spanish-cedar (*Cedrela odorata*) in harvest gaps and skid trails. *Ejido* members collected seeds of these species, grew them in nurseries and conducted the outplanting in post-harvest stands.

A number of studies (Dickinson *et al.* 2000, Negreros-Castillo & Mize 2003, Snook & Negreros-Castillo 2004) have shown that the limited sizes of canopy openings created by timber harvesting do not provide enough light for survival and growth of planted or natural seedlings of mahogany. Only in openings the size of log landings (0.2–1.0 ha in area) did planted mahogany seedlings show good survivorship and rapid height growth (Richards 1991, Snook 2005). Based on these observations, large experimental clearings have been established using a range of techniques (felling, slash-and-burn clearing, machine uprooting, partial overstorey removal), combined with both sowing seed and planting seedlings of mahogany (Negreros-Castillo & Mize 1993, Negreros-Castillo *et al.* 2003, Snook & Negreros-Castillo 2004).

A modification of these silvicultural approaches could be to rely on natural seedfall from mahogany seed trees retained during harvests and focusing treatments on creating open-canopy conditions in the vicinity of mahogany seed trees. Then it may be possible to rely on the wind dispersal of seed, eliminating the costs of nursery and planting programmes (Negreros-Castillo & Mize 1993, 2003, Snook & Negreros-Castillo 2004). Information about seed production and seed dispersal area is critical for designing the appropriate silvicultural methods.

For tree species with wind-dispersed seeds such as mahogany, wind direction and speed are generally the main factors controlling the spatial pattern of seed dispersal (Nathan & Muller-Landau 2000). In a study in eastern Brazil, the dispersal directions for mahogany were found to match with the dominant trade winds (Grogan & Galvão 2006). However, a study of African mahogany (*Entandrophragma* spp.) in the Central African Republic (Medjibe & Hall 2002) found that seed dispersal was not controlled by wind direction; rather, the seedfall directions were correlated to the orientation of large spreading branches of each tree. Other studies have shown that seasonal prevailing winds may not always be the most important determinant of seed dispersal patterns. Instead infrequent but very strong winds may have the greatest effect on dispersal (Stewart *et al.* 1998).

A recent study of mahogany seed production over a six-year period was conducted in the *ejido* forests of central Quintana Roo (Cámara-Cabrales 2005, Snook *et al.* 2005). Our research adds to this earlier work by focusing on the pattern of mahogany seed dispersal (distance, direction and quantity) from mature mahogany trees in *ejido* forests in the same region. We examined seed dispersal patterns for 11 trees chosen from a range of 55 to >100 cm dbh. This diameter range was chosen to include trees that would likely be retained temporarily as seed trees (55–75 cm dbh) during operational harvests.

The objectives of this study were (1) to determine the distance, direction and quantity (seed density) of seed dispersal from mahogany trees in Quintana Roo forests, and compare these patterns with wind data for the dispersal period, and (2) to test how tree size affects these dispersal patterns. The implications of these results are then described in the context of designing regeneration methods that use natural seedfall for establishing mahogany regeneration.

MATERIALS AND METHODS

Description of study site and forest type

This research was conducted in the *ejido* Naranjal located at 19° 21' N and 88° 27' W in the state of Quintana Roo, Mexico. The region is part of the flat or gently rolling limestone Yucatán plain, with karst topography. Soils are fertile, with a pH of 6.4–7.5, and overlie a friable marl subsoil. Precipitation is 1200–1500 mm year^{-1}, with a mean annual temperature of 24–26 °C. The heaviest rainfall is from May to October; the dry season lasts from February to May, with March and April having the lowest precipitation (Escobar-Nava 1986). The dominant trade winds throughout the year are from the south-east and east, but winds from the north (called *nortes*) also occur periodically between November and May.

This region is within the seasonal dry forest zone (Lamb 1966, Patiño-Valera 1997). The forest is semi-evergreen, with many species (including mahogany) being leafless during the dry season. Hurricane winds are the most common natural disturbance in this forest region, with shifting agriculture (*milpa*) being the major human-mediated disturbance. A forest inventory of the large *ejido* Noh Bec, which is near to Naranjal, reported 119 tree species in the 6600 ha of the inventory, with a mean of 658 trees ha^{-1} and 23 m^2 ha^{-1} basal area for trees ≥ 10 cm dbh (Arguelles *et al.* 1998). In this region, zapotillo (*Pouteria reticulata)*, chicle or chicozapote (*Manilkara zapota)*, and ramon (*Brosimum alicastrum)* are the most common tree species (Vester & Navarro-Martínez 2005). The Noh Bec inventory showed that mahogany density was 6.9 trees ha^{-1} for trees 10–54 cm dbh and 1.0 trees ha^{-1} for trees > 55 cm dbh (Arguelles *et al.* 1998). A broader inventory of a set of *ejidos* in Quintana Roo (Patiño-Valera 1997) found similar results with mahogany trees ≥ 15 cm dbh occurring at mean densities of 6.4 trees ha^{-1}; for trees > 50 cm, the density was 1.0 trees ha^{-1}.

Mahogany fruits initiate development at the beginning of the rainy season (May) and they mature 9–11 months later during the dry season. The fruit is a large (12–18 cm long) pear-shaped woody capsule divided into five segments (pericarps). Each fruit contains about 45 fully developed winged seeds (Rodríguez-Santiago *et al.* 1994), densely packed around a central columella. Seeds are approximately 1 cm long with a wing of 6 cm in length and a dry weight of 0.54 g seed^{-1} (Patiño-Valera 1997). During the dry season, the five woody pericarps dehisce and fall to the ground beneath the tree crown. Seeds are then gradually dispersed from the columella. Mahogany seeds either germinate shortly after seedfall with the onset of the rains, or lose their viability within a few months (Morris *et al.* 2000).

Data collection

In February 2002, 11 mahogany trees were selected in managed forest areas of the *ejido* Naranjal to span the dbh range of 50 to 100 cm. The previous management had consisted of a harvest of mahogany trees ≥ 75 cm dbh in some parts of the forest, but larger trees were present in other parts. The 11 trees were widely distributed throughout the Naranjal forest and each sample tree was a minimum distance of 100 m from any other mahogany tree that had produced fruit that year. The sample trees were all in dominant canopy positions. For each tree, measurements were made for tree height (clinometer to 0.1 m precision), dbh (tape to 0.1 cm) and crown radius (tape to 0.1 m). Crown radii (r) were measured along each of the eight cardinal directions from the stem and crown projection area (CPA) was calculated using the mean-radius equation

$$CPA = [\sum(r^2)/8] * \pi$$

For each tree, two kinds of plots were established, namely, 'fruit plots' to determine the amount and spatial pattern of fruit and seed production in the crown, and 'seed plots' to determine the density and spatial pattern of seedfall beneath and surrounding the crown. Fruit plots were 1 × 2 m in size and were distributed under the tree crown using randomly selected directions and distances (thus, the plots were located from 1 to 9 m from the tree stem). The number of fruit plots used for each tree was determined such that the total sample area was at least 10% of the CPA of the tree. The number of fruit pericarps in each plot was counted and divided by five (to account for the five pericarps contained in each fruit) to obtain the mean number of fruits tree^{-1} (Grogan & Galvão 2006, Snook *et al.* 2005).

Seed plots were 1 × 1 m in size and were placed along eight transects radiating from the stem of each sample tree, following the compass directions N, NE, E, SE, S, SW, W, NW. Transect lengths were a maximum of 60 m. Seed plots were located at random distances along each transect with a minimum distance of 1 m between them. There were 15 to 34 seed plots located on each transect with a mean of 180 seed plots per tree (there were fewer seed plots along transects with repeated zero counts with increasing distance from the tree). Measurements were made 5 to 25 days after seed dispersal ended. In each seed plot, the leaf litter was removed by hand and the seeds were counted and categorized as (1) viable, (2) not fully developed, (3) destroyed by predators and (4) destroyed by fungi.

The weather station nearest to the study site is at the city of Chetumal, about 100 km to the south. Data from that station were obtained for frequency of wind direction and mean wind speed for 1 February through 30 April 2002, which approximated the mahogany dispersal period for this study.

Data analysis

Although tree size (as measured by dbh) is a continuous variable, the sample of 11 trees was divided into two groups (< 75 cm and ≥ 75 cm dbh) because 75 cm dbh was found to be an approximate inflection point at which there is a curvilinear increase in crown volume and seed production with increasing dbh (Snook *et al.* 2005). Seed dispersal data from the seed plots were displayed as seed shadow graphs using two variables graphed along the eight cardinal directions: (1) the per cent of the total dispersed seed distributed in each direction and (2) the maximum distance that seeds were dispersed in each direction. The two variables were calculated for each direction for each tree and then means were calculated for each of the two tree size classes. The dispersal area for each tree was calculated using the same mean–radius equation as for CPA, where the radius was the maximum dispersal distance in each of the eight directions.

JMP IN software (SAS Institute 1996) was used for all statistical analyses. One-way ANOVA methods were used to compare the variables of maximum dispersal distance and per cent distribution among directions within each tree size class and between the two tree size classes. If the ANOVA was significant ($p < 0.01$), Tukey-Kramer HSD post-hoc means separation tests were used at $p = 0.05$. The dispersal data (seeds m^{-2}) were aggregated across trees in 1 m units from the tree stem to the transect end. Graphs of seeds m^{-2} along the transects (dispersal curves) were modelled by negative exponential regression.

RESULTS

Tree dimensions and fruit production

The 11 sample trees formed a continuous distribution in size from 57.5 to 101.7 cm dbh (Table 1). The large tree class (≥ 75 cm dbh) had a mean height that was only 1.6 m taller than the small tree class (< 75 cm dbh), but had significantly larger mean crown projection area (38% greater). The large tree class produced nearly twice as many fruits tree^{-1} as the small class (Table 1), but the variability was high, so there was no significant difference between size classes ($p = 0.20$). This variability was due in part to two outlier trees: tree number 7 in the small size class produced 222 fruits, four to six times more than the other trees in that class, which had a mean of 75 fruits tree^{-1}, and tree number 13 in the large class produced 47 fruits, which was two to four times less than the other trees in its class, which had a mean of 133 fruits tree^{-1}. The spatial distribution of fruit capsules on the ground beneath the crowns was analysed to determine if fruits developed in a uniform pattern throughout the crown areas. There were no significant differences among the eight directions ($p = 0.598$) for either tree size class.

Wind characteristics

During the dry season (1 February to 30 April) of 2002, winds were from E and SE for 82% of the time, which is the direction from which the prevailing trade winds blow (Figure 2). The *nortes* winds from NW, N and NE occurred for 17% of the period, and the other directions collectively had only 1% frequency. Mean wind speed was 2.5 to 4.3 m s^{-1} for all wind directions except for SE, which had a mean of 7.6 m s^{-1}.

Table 1 Dimensions and fruit production in 2002 of the 11 mahogany (*Swietenia macrophylla*) seed trees studied for dispersal in Quintana Roo, Mexico

Tree number	Dbh (cm)	Height (m)	Mean crown radius (m)	CPA (m^2)	Fruits (number tree^{-1})	Seeds (number tree^{-1})
			Trees < 75 cm dbh			
1	57.5	19.7	4.5	62.7	57	2545
10	58.0	25.3	5.3	127.2	52	2349
7	59.0	22.5	5.5	102.0	222	9983
11	62.4	21.3	6.5	136.0	39	1746
14	62.7	26.7	6.6	146.9	36	1633
12	69.4	24.6	5.4	128.8	44	1965
Mean	61.5	23.4	5.7	119.0	75	3370
(SE)	(1.7)	(1.0)	(0.3)	(10.0)	(72)	(1214)
			Trees ≥ 75 cm dbh			
2	76.4	22.6	6.8	162.0	102	4592
13	76.4	23.4	5.9	127.7	47	2123
5	77.2	26.6	6.7	155.5	216	9742
3	90.4	22.5	7.7	205.0	116	5240
9	101.7	29.4	6.6	167.1	184	8271
Mean	84.4	25.0	6.8	164.0	133	5994
(SE)	(4.5)	(1.2)	(0.3)	(11.8)	(67)	(1212)

Means and standard errors (SE) are shown for each tree size class.

Timing and spatial distribution of seed dispersal

The dry season came somewhat later than normal in the study area in 2002. Rains continued through February and occasionally into March, so the fruits did not all dry and dehisce in March and April as expected. Seed dispersal in 2002 extended from mid-March to mid-May and the timing of dispersal varied among the 11 sample trees.

The greatest proportion of seeds was dispersed in the NW, W and SW directions (Figure 3a). Seed dispersal in these directions was significantly greater ($F_{(7,80)} = 19$, $p < 0.0001$) than the other five directions in both tree size classes but this skewed pattern was more extreme in the small class. The direction of seed dispersal was different between the large and small tree classes ($F_{(5,27)} = 37$, $p < 0.0001$). The small class had significantly greater seed percentage in the NW, W and SW directions as a group than was found for the same directions for the large class. The small size class had a significantly lower percentage in the S, SE and E directions as a group than the large class. The large and small size classes were similar for dispersal in the N and NE directions (HSD mean comparisons, $p < 0.05$).

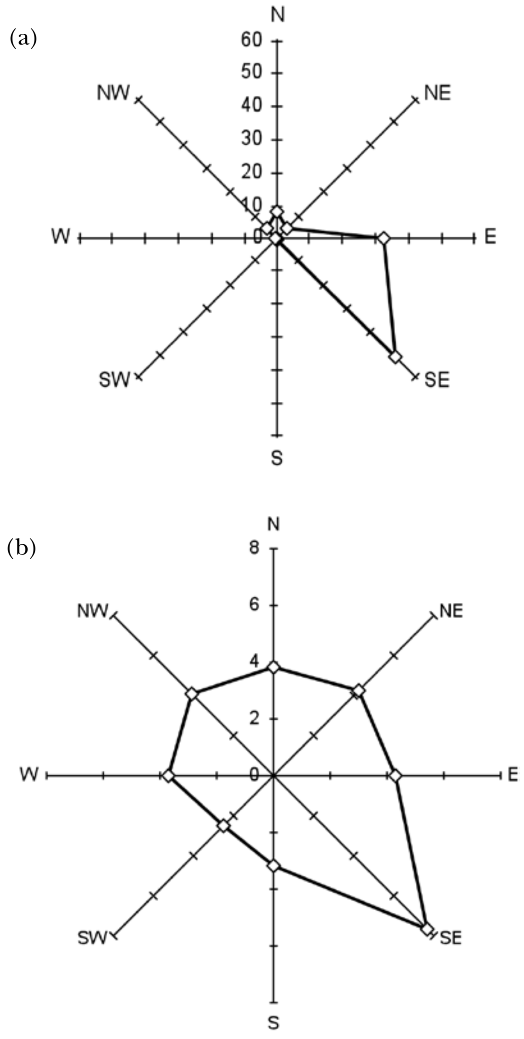

Figure 2 (a) Frequency of wind direction (%) and (b) mean wind speed by direction (m s^{-1}) for the period 1 March to 30 April 2002 at Chetumal, Quintana Roo, Mexico

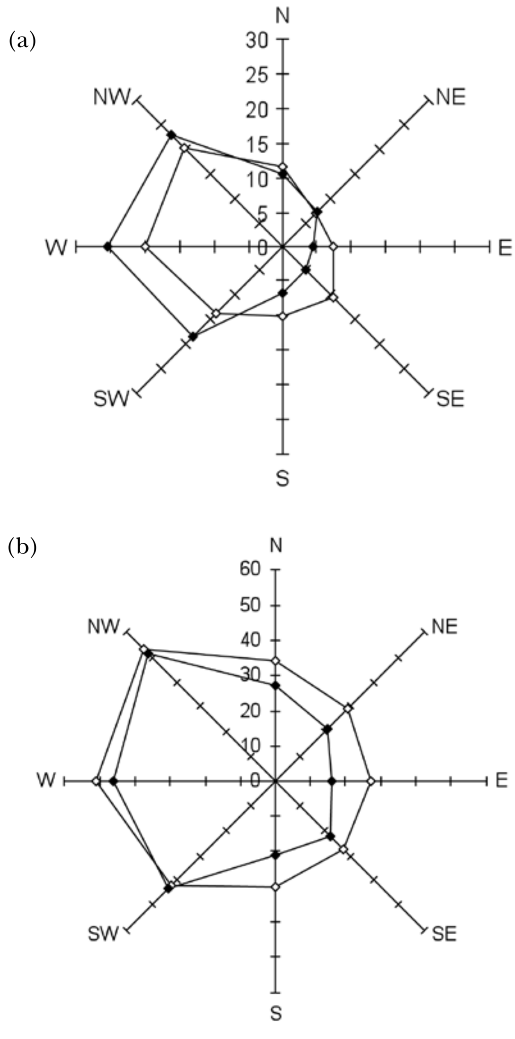

Figure 3 (a) Mean proportional distribution of total seedfall by direction (%) and (b) mean maximum dispersal distance (m) of 11 mahogany (*Swietenia macrophylla*) seed trees in Quintana Roo, Mexico. Black squares are six trees < 75 cm dbh and white squares are five trees ≥ 75 cm dbh.

Mean maximum dispersal distance was also significantly different among directions ($F_{(7,80)} = 26$; $p < 0.0001$). Dispersal was greater in the directions NW, W and SW compared with other directions (Figure 3b). Dispersal distances for these three directions were similar between the two tree size classes, but the dispersal distance for the large tree class was greater than that of the small class for the other five directions, and significantly greater for S, SE, and E (HSD mean comparisons, $p < 0.05$).

Dispersal area and seed density

The mean dispersal area (defined by the seed shadow polygons in Figure 3(b) was 0.47 ha for large trees and 0.37 ha for small trees. This is a conservative estimate of dispersal area because it was based on the greatest distance that a seed was found in a sample plot in each transect direction for each tree. It was observed that a small number of seeds were dispersed beyond the 60 m transect length.

Due to the differences in dispersal proportion and distance among directions, two dispersal curves (Figure 4) were constructed for each tree size-class: one for the high-dispersal directions as a group (NW, W, SW) and one for the low-dispersal directions as a group (S, SE, E, NE, N). These were modelled with the commonly used negative exponential form (Willson 1993). However, high-dispersal directions for the large tree class showed a linear pattern ($r^2 = 0.84$) mainly because of the lack of high seed density numbers beneath and near tree crowns. For high-dispersal directions, the large trees had 3 to 4.5 seed m^{-2} within 20 m of the stem and a mean of > 1 seed m^{-2} extending to 45 m from the stem, with the density approaching zero at 60 m. The high-dispersal curve for the small tree class ($r^2 = 0.83$) showed somewhat greater seed densities (4 to 6 seeds m^{-2}) close to the tree, but seed density declined more steeply with distance, so a mean of > 1 seed m^{-2} extended only to 30 m from the stem and approached zero just beyond 50 m. The median dispersal distance (the distance within which 50% of the seeds had been dispersed) was 30 m for large trees and 22 m for small trees for the NW, W, SW high-dispersal directions. For the low-dispersal curve of the small tree class ($r^2 = 0.73$), seed density was consistently one-half

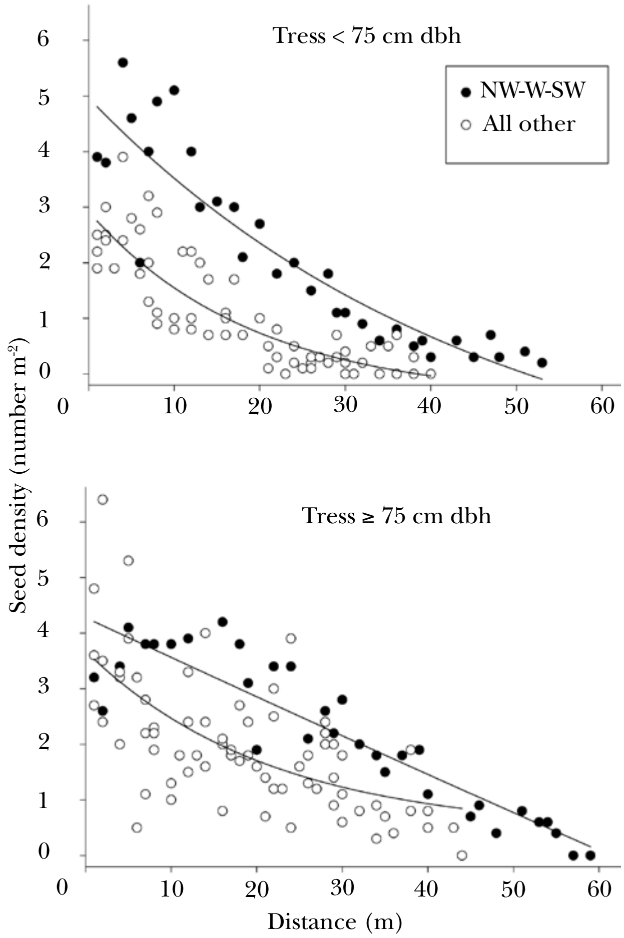

Figure 4 Mean seed density as a function of distance from the parent tree for two tree size classes and two groups of directions (NW–W–SW for high dispersal and all other directions for low dispersal) for 11 mahogany (*S. macrophylla*) seed trees studied in Quintana Roo, Mexico

or less of the seed density of the high-dispersal directions along the dispersal curve. The same general pattern occurred for the low-dispersal curve of large trees, but the variability was much greater ($r^2 = 0.45$). The median dispersal distances in the low dispersal directions were 27 m for large trees and 15 m for small trees.

Seed health condition

The condition of seeds when they were collected from seed dispersal plots was as follows: 75% viable seeds, 20% not fully developed, 4% destroyed by predators and < 1% destroyed by fungi.

DISCUSSION

Tree dimensions and fruit production

The larger size class of trees (≥ 75 cm dbh) produced twice as many fruits in 2002 as the smaller trees (< 75 cm dbh), although the difference was not statistically significant because of high variability. The independent measurement of total dispersed seeds corroborated that finding, with just over twice as many seeds in the dispersal area of the large tree class compared with the small trees. Mahogany fruit production had been studied in the same region for six years (1997–2002), with a larger sample of 83 trees (Snook *et al.* 2005). Those results showed that the large size class trees had significantly greater fruit production than the small class, but also showed the same high variability that was observed among the 11 trees in the current study. In the six-year study, the overall size of the mahogany fruit crop varied among years. The largest crop occurred in 1998 and the smallest crops were in 1999 and 2000. The 2002 seed crop (used in this study) was close to the six-year average.

Seed dispersal: direction and distance

The seed dispersal patterns of the 11 trees in this study appeared to be strongly affected by prevailing winds. The percentage distributions of seeds of both sizes of trees were strongly skewed to the NW–W–SW directions, which corresponded to the highest frequency of wind direction (E and SE) and the highest wind speeds (SE). There was very little wind from the S–SW–W directions and the lowest seed density occurred in the corresponding directions N–NE–E. The *nortes* winds from NW–N–NE (which have substantially lower frequency of occurrence than trade winds) showed moderate seed dispersal for S–SE. The only anomaly in the wind and dispersal data was that the SW direction had high dispersal (similar to the NW–W directions from the trade winds) but the wind from the NE was much less frequent than the E–SE trade winds. This anomaly may be a consequence of the wind measurements having been taken 100 km away from the forest study site.

The prevailing trade winds appeared to have greater effects on the dispersal from small trees than from large trees. The proportion of total seeds was more strongly skewed to the west and the maximum dispersal distance was lower to the east for the small tree class. There was also greater variability of seed density with distance for large trees. The large and small tree classes had little difference in height, but the larger diameter trees had larger crowns and were likely older, with crowns that were in more emergent canopy positions. The *nortes* winds and local turbulence may have had a greater effect on larger trees with more exposed crowns, increasing the directional variability, whereas the stronger and more consistent trade winds may have had greater effects on smaller trees, with crowns located within the closed canopy.

To our knowledge, the only previous study of mahogany seed dispersal in Quintana Roo was for a single tree that was 30 m in height and located within an area cleared of other trees (Rodríguez-Santiago *et al.* 1994). In that study, 81% of the seeds were dispersed in the western half of the sample area, within a maximum distance of 60 m. Grogan and Galvão (2006), working in eastern Brazil, found a similar skewed seed shadow with the greatest dispersal to the west (with SE and E trade winds similar to Quintana Roo). Seed density approached zero at 60 to 75 m in the SW–W–NW directions and at 24 to 42 m in the NE–E–SE directions. The maximum distance of mahogany seed dispersal was 80 m in the Bolivian Amazon (Gullison *et al.* 1996); greater seed densities were to the S and SE directions, but no information on wind patterns was given.

Mahogany seed dispersal occurred beyond these distances, with seed shadow areas reported from 1.6 (Grogan & Galvão 2006) to 4 ha (Lamb 1966). However, the outer portions of these large areas contained very low densities of seeds. Long-distance dispersal is important for potential gradual expansion of species' range and possibly for escaping density-dependent seed predation, but for silvicultural purposes, the dispersal area with measurable seed density (~ 0.5 seeds m^{-2}) is of greatest importance.

Seed on the forest floor can be destroyed by a large number of seed predators, including mammals, invertebrates and fungal pathogens. In this study, seed predation was observed only 5–25 days after all seeds were dispersed. Only 5% of dispersed seeds were observed as having been destroyed by predators but others may have been removed from plots by small mammals and thus were not included in the predation rate. A study in Quintana Roo found 20% loss of mahogany seeds to predators over a 5-month period (Negreros-Castillo *et al.* 2003) and another in Para, Brazil found 40% loss, also over 5 months (Grogan & Galvão 2006). Research in Brazil (Grogan & Galvão 2006, Norghauer *et al.* 2006) found no differences in seed predation rates as a function of distance from the tree or in gaps as compared with closed canopies. Thus, the spatial pattern of dispersal measured in this study soon after dispersal would likely be similar to those that have been studied after longer exposure to predators; however, the overall seed numbers would likely be substantially lower.

Implications for silvicultural practice

This study provides information for designing silvicultural methods that incorporate natural seed dispersal from mahogany seed trees as the source of regeneration in sustainable forest management. The current regeneration methods used in the *ejido* forests of Quintana Roo rely upon enrichment planting of mahogany and Spanish-cedar in harvest gaps and skid roads. However, the conditions that promote seedling survival and growth occur in larger clearings. An open area of 500 m^2 provides adequate survival but seedling growth rates continue to increase with increasing clearing size up to 5000 m^2 (Snook 2005). A principal focus of recent research has been on testing methods of overstorey felling and site preparation to create these clearings (Snook & Negreros-Castillo 2004, Negreros-Castillo *et al.* 2003).

Mahogany has been established by dispersal from seed trees as part of operational harvesting but this has generally been limited to retaining seed trees upwind of log landings large enough to provide adequate light for seedling growth (Richards 1991, Snook *et al.* 2003). A more comprehensive system had been established much earlier in Belize, involving a shelterwood method with two cuts (Stevenson 1927). The first cut created an open or partially open clearing, with the retention of seed trees. After regeneration had been established and had grown to sufficient size, some or all of the valuable overstorey seed trees were removed in the second cut and the seedlings or saplings were weeded. Thus, there has been some operational experience with silvicultural systems that incorporate natural seed dispersal as the main source of regeneration.

The information provided by this study showed that mahogany seed trees > 55 cm dbh have seed dispersal areas of ~ 4000–5000 m^2. This is similar to the critical minimum clearing size that promotes rapid seedling development. Further, it showed that the clearing treatment area should not be entirely downwind (to the NW–W–SW directions) of a seed tree; dispersal was approximately 50 m to the westerly directions and 20–30 m to all other directions. This suggests that a seed-tree system could be employed for regeneration by applying one of the successful clearing methods within the seed dispersal area, retaining only the mahogany seed tree. The valuable mahogany tree would then be harvested in a second cut after sufficient seed years have occurred to produce adequate numbers of well-established regeneration. Alternatively, the clearing could be made using a shelterwood method rather than the complete clearing of a seed-tree method. The additional trees retained in a shelterwood would likely be valuable timber trees that have not yet reached the target diameter for harvest. However, the retained shelterwood canopy would need to have a low basal area to avoid interference with regeneration (Negreros-Castillo & Mize 1993).

The mahogany shoot-borer (*Hypsipyla grandella*) is the most damaging insect that affects mahogany seedlings and must always be considered when designing silvicultural treatments. Seedlings are protected from shoot-borers when growing beneath a closed canopy but after the first year seedling growth and survival declines rapidly under a canopy (Grogan & Galvão 2006). Lateral shade from partial overstories (as in a shelterwood stand) or from dense young secondary vegetation growing with the mahogany seedlings can reduce the rate of shoot-borer attacks (Snook & Negreros-Castillo 2004, Grogan *et al.* 2005).

Generally, seed-tree or shelterwood systems treat a cutting area uniformly, leaving an open stand with widely spaced seed trees. However, the pattern of harvest could be patchy across the cutting area, with clearings being made only around selected seed trees. It would also be possible to create clearings in patches where there are no seed trees, using direct seeding to establish regeneration, thus, creating a mixture in a stand of both seed-tree/shelterwood and direct-seeding patches.

The use of a natural seed dispersal method on at least some forest areas would reduce the level of seed collection, nursery operations, transportation and planting. Research results have made it clear that overstorey canopy opening and site preparation are needed for successful establishment of regeneration, whether natural seed dispersal or planting is used. Substantial resources are required to carry out those clearing treatments because most of the trees to be cut are small and have little timber value. Thus, reducing artificial regeneration operations may be helpful in limiting overall silvicultural treatment costs.

However, regulatory problems exist in moving the experimental findings to operational trials, both for creating large openings by cutting trees that are smaller than the specified minimum harvest diameter and for using natural seedfall rather than the required enrichment planting. Special permits would be required for these steps (Snook 2005). Further details of costs and regulatory issues are beyond the scope of this paper.

It should be noted that the potential for using silvicultural methods that rely on natural seedfall exists in some parts of the Yucatán Peninsula because of the relatively high density of mahogany (mean density of 7 trees ha^{-1}, 10 cm dbh) (Arguelles *et al.* 1998). Mahogany tree abundance varies greatly across Quintana Roo, largely depending on past harvests, but it has greater abundance on some *ejido* lands than in many other parts of its natural range. The long-term effects of hurricane damage and shifting agriculture methods of the local Mayan communities have created open conditions that favoured mahogany regeneration in some areas. In most other regions within the range of mahogany (particularly in the Amazon Basin), the density of mahogany trees > 10 cm dbh is generally 0.1 to 0.5 trees ha^{-1} (Brown *et al.* 2003), which would not be sufficient for a seed-tree or shelterwood system.

Furthermore, the limestone-derived soils in the Yucatán provide high nutrient status over large areas. In contrast, mahogany is limited in area by soil conditions in the Amazon and in central Africa (with *Entandrophragma* spp. in the latter case). In these cases, mahogany becomes a microsite specialist, growing principally on nutrient-rich soils that occur only on the low ground near streams (Grogan *et al.* 2003, Hall *et al.* 2004). In these areas, enrichment planting may be the best approach for regeneration, by assuring that seedlings are established on the best soils for long-term mahogany survival and growth.

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REFERENCES

Arguelles SAL, Sánchez RF, Caballero RA & Ramirez S. 1998. Programa de manejo forestal para el bosque tropical del ejido noh bec 1998–2008. (Unpublished)

Bray DB, Merion-Pérez L, Negreros-Castillo P, Segura-Warnholtz G, Torres-Rijo JM & Vester HFM. 2003. Mexico's community-managed forest as a global model for sustainable landscapes. *Conservation Biology* 17: 672–677.

Bray DB & Klepeis P. 2003. Deforestation, forest transitions, and institutions for sustainability in southeastern Mexico, 1900–2000. *Environment and History* 11: 195–223.

Brown N, Jennings S & Clements T. 2003. The ecology, silviculture and biogeography of mahogany (*Swietenia macrophylla*: a review of the evidence. *Perspectives on Plant Ecology, Evolution, and Systematics* 6: 37–49.

Cámara-Cabrales L. 2005. Seed production, seed dispersal, and seedling ecology of mahogany (*Swietenia macrophylla* King) in Quintana Roo, Mexico. PhD dissertation, University of Massachusetts, Amherst.

Dickinson MB, Whigham DF & Hermann SM. 2000. Tree regeneration in felling and natural treefall disturbances in a semideciduous tropical forest in Mexico. *Forest Ecology and Management* 134: 137–151.

Escobar-Nava A. 1986. *Geografía General del Estado de Quintana Roo.* Second edition. Fondo de Fomento Editorial del Estado de Quintana Roo, Chetumal.

Grogan J & Galvão J. 2006. Factors limiting post-logging seedling regeneration by big-leaf mahogany (*Swietenia macrophylla*) in southeastern Amazonia, Brazil, and implications for sustainable management. *Biotropica* 38: 219–228.

Grogan J, Ashton MS & Galvão J. 2003. Big-leaf mahogany (*Swietenia macrophylla*) seedling survival and growth across a topographic gradient in southeast Pará, Brazil. *Forest Ecology and Management* 186: 311–326.

Grogan J, Landis RM, Ashton MS & Galvão J. 2005. Growth response by big-leaf mahogany (*Swietenia macrophylla*) advance seedling regeneration to overhead canopy release in southeast Pará, Brazil. *Forest Ecology and Management* 204: 399–412.

Gullison RE, Panfil SN, Strouse JJ & Hubbell SP. 1996. Ecology and management of mahogany (*Swietenia macrophylla* King) in the Chimanes forest, Beni Bolivia. *Botanical Journal of the Linnean Society* 122: 9–34.

Hall JS, McKenna JJ, Ashton PMS & Gregoire TG. 2004. Habitat characterizations underestimate the role of edaphic factors controlling the distribution of *Entandrophragma*. *Ecology* 85: 2171–2183.

Lamb BF. 1966. *Mahogany of Tropical America: Its Ecology and Management.* The University of Michigan Press, Ann Arbor.

Medjibe V & Hall JS. 2002. Seed dispersal and its implications for silviculture of African mahogany (*Entandrophragma* spp.) in undisturbed forest in the Central African Republic. *Forest Ecology and Management* 170: 249–257.

Morris M, Negreros-Castillo P & Mize CW. 2000. Sowing date, shade, and irrigation affect big-leaf mahogany (*Swietenia macrophylla* King). *Forest Ecology and Management* 132: 173–181.

Nathan R & Muller-Landau HC. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15: 278–285.

Negreros-Castillo P & Mize C. 1993. Effects of partial overstory removal on the natural regeneration of tropical forest in Quintana Roo, Mexico. *Forest Ecology and Management* 58: 259–272.

Negreros-Castillo P & Mize C. 2003. Enrichment planting of big-leaf mahogany and Spanish cedar in Quintana Roo, Mexico. Pp. 278–287 in Lugo AE *et al.* (Eds.) *Big-Leaf Mahogany: Genetics, Ecology, and Management.* Springer-Verlag, New York.

Negreros-Castillo P, Snook LK & Mize C. 2003. Regenerating mahogany (*Swietenia macrophylla)* from seed in Quintana Roo, Mexico: the effects of sowing method and clearing treatment. *Forest Ecology and Management* 183: 351–362.

Norghauer JM, Malcolm JR, Zimmerman BL & Felfili JM. 2006. An experimental test of density- and distant-dependent recruitment of mahogany (*Swietenia macrophylla)* in southeastern Amazonia. *Oecologia* 148: 437–446.

Patiño-Valera F. 1997. *Recursos Geneticos de Swietenia y Cedrela en los Neotropicos: Propuestas para Acciones Coordinadas.* FAO, Rome.

Richards EM. 1991. The forest *ejidos* of south-east Mexico: a case study of community based sustained yield management. *Commonwealth Forestry Review* 70: 290–311.

Rodríguez-Santiago B, Chavelas-Polito J & Garcia-Cuevas X. 1994. Disperson de semillas y establecimiento de caoba (*Swietenia macrophylla* King) despues de un tratamiento mecanico del sitio. Pp. 81–90 in Snook LK & Barrera de Jorgenson A (Eds.) *Madera, Chicle, Caza y Milpa. Contribuciones al Manejo Intergral de las Selva de Quintana Roo.* INIFAP, Merida.

Shono K & Snook LK. 2006. Growth of big-leaf mahogany (*Swietenia macrophylla*) in natural forests in Belize. *Journal of Tropical Forest Science* 18: 66–73.

Snook LK. 2003. Regeneration, growth and sustainability of mahogany in Mexico's Yucatán forests. Pp. 169–192 in Lugo A, Figueroa-Colon J & Alayon M (Eds.). *Big-Leaf Mahogany: Genetics, Ecology and Management.* Ecological Studies 159. Springer Verlag, New York.

Snook LK. 2005. Sustaining mahogany: research and silviculture in Mexico's community forests. *Bois et Forets des Tropiques* 285: 55–65.

Snook LK & Negreros-Castillo P 2004. Regenerating mahogany (*Swietenia macrophylla* King) on clearings in Mexico's Maya forest: the effect of clearing method and cleaning on seedling survival and growth. *Forest Ecology and Management* 189: 143–160.

Snook LK, Cámara-Cabrales L & Kelty MJ. 2005. Six years of fruit production by mahogany trees (*Swietenia macrophylla*): patterns of variation and implications for sustainability. *Forest Ecology and Management* 206: 221–235.

Snook LK, Santos-Jimenez VA, Carreón-Mundo M, Chan-Rivas C, May-Ek FJ, Mas-Kantún P, Hernández-Hernández C, Nolasco-Morales A & Escobar-Ruíz C. 2003. Managing natural forests for sustainable harvests of mahogany (*Swietenia macrophylla*): experiences in Mexico's community forests. *Unasylva* 54: 68–73.

Stevenson NS. 1927. Silvicultural treatment of mahogany forests in British Honduras. *Empire Forest Journal* 6: 219–227.

Stewart JD, Hogg EH, Hurdle PA, Stadt KJ, Tollestrup P & Lieffers VJ. 1998. Dispersal of white spruce in mature aspen stands. *Canadian Journal of Botany* 76: 181–188.

Vester HFM & Navarro-Martínez MA. 2005. Ecological issues in community tropical forest management in Quintana Roo, Mexico. Pp. 183–214 in Bray DB *et al.* (Eds.) *The Community Forests of Mexico: Managing for Sustainable Landscapes.* University of Texas Press, Austin.

Willson MF. 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107/108: 261–280.