

Competition among surface roots in a selectively-logged, semi-deciduous forest in southeastern Mexico – effects on seedlings of two species of contrasting shade tolerance

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ABSTRACT.-- Experimental manipulations of root competition on naturally established seedlings were conducted across canopy openness and soil depth gradients in a selectively-logged, semideciduous forest on limestone-derived soils in southeastern Mexico. We studied the relatively shade intolerant mahogany (*Swietenia macrophylla*, Meliaceae) and shade tolerant ramón (*Brosimum alicastrum*, Moraceae). Both species are ecologically and economically important canopy trees that respond differently to selective logging, hurricanes, and fires on the Yucatan Peninsula. The canopy openness gradient used in the experiment was created by low-intensity selective logging operations. The responses of naturally occurring seedlings of both species growing within 20-30 cm deep circular trenches were examined over a 19-month experimental period. Trenching resulted in increased relative growth in diameter, stem length, and number of leaves of *Swietenia* compared with controls, but had no effect on *Brosimum* relative growth or on seedling survival of either species. There was no significant interaction between increased light availability and trenching on *Swietenia* seedlings, perhaps because of their larger size in gaps. Trenching effects on *Swietenia* were not greater during the dry season, suggesting that surface trenching affected growth during transitions between seasons. Contrasting responses of *Swietenia* and *Brosimum* seedlings to changes in soil and light environments point to the need for diversity in silvicultural practices in seasonally-dry tropical forests such as the community-managed forest examined in this study.

KEYWORDS.-- *Brosimum alicastrum*, *Swietenia macrophylla*, trenching, regeneration

INTRODUCTION

Infrequent large-scale events (fire and hurricanes) and selective logging characterize the disturbance regime broadly over the southern and eastern portions of the Yucatan Peninsula (see Lamb 1966, Snook 1996, Whigham *et al.* 1998, Whigham *et al.* 1999, Dickinson *et al.* 2000b, Whigham *et al.* 2003). The region's forests are characterized by a mix of evergreen and dry-season deciduous tree species (Pennington and Sarukhan 1968, Snook 1993). Between major events, canopy disturbance rates are exceedingly low and are caused by small-scale tree fall events (Dickinson *et al.* 2000a). In southeastern Mexico, past logging has targeted a group of relatively shade-intolerant species that were often abundant because of fire (e.g., *Swietenia*). Fires in the region's forests are typically surface and ground (smoldering) fires that can cause extensive mortality and increased light and,

presumably, soil resource levels for seedlings and basal and root sprouts (Snook 1993, 1996).

Because of poor natural regeneration of *Swietenia macrophylla* (big-leaf mahogany [King, Meliaceae]), enrichment planting has been practiced consistently in an effort to ensure adequate regeneration (Dickinson and Whigham 1999). Nonetheless, as large individuals of historically valuable species are depleted, efforts are being made to market new timber species (Galletti 1998, Taylor and Zabin 2000). *Brosimum alicastrum* (ramón [Swartz., Moraceae]) is one of these and contrasts with *Swietenia* in that it gains a relative advantage after hurricanes and small-scale canopy gaps, canopy disturbances through which its seedlings and saplings, abundant below a closed canopy, often survive (Dickinson *et al.* 2000b, Snook 1993). In this study, we examined the effects of root competition on *Swietenia* and *Brosimum* seedlings. Although both species' seeds

germinate in the shade, *Brosimum* is more shade tolerant (Ramos and Grace 1990).

In seasonally-dry forests, seedling growth and survival is affected not only by light but also by soil-resource availability (e.g., Gerhardt 1996a, 1996b, Coomes and Grubb 2000, Barberis and Tanner 2005). *Swietenia* seedlings would be expected to respond more quickly to improved light and soil moisture conditions than *Brosimum* because of their higher potential growth rates and greater plasticity in physiological rates (Ramos and Grace 1990). Strauss-Debenedetti and Bazzaz (1991) and Strauss-Debenedetti and Berlyn (1994) showed that *Brosimum* seedlings have low to moderate plasticity in leaf anatomy and physiological rates when moved from low to high light. Ramos and Grace (1990) found lower plasticity in resource allocation between roots and shoots in *Brosimum* than *Swietenia* seedlings grown at different light levels. Thick leaves and low plasticity in root-shoot ratios have been found to correlate with tolerance for both low light and periodic drought (Coomes and Grubb 2000). *Brosimum* root-shoot ratios are not only relatively static, but also are higher than those of *Swietenia* (Ramos and Grace 1990), a trait which would reinforce drought tolerance. For *Swietenia* seedlings limited by low light during the wet season, highly plastic allocation of limited photosynthetic energy and lower root-shoot ratios would be expected to lead to soil resource limitation during dry seasons (e.g., Smith and Huston 1989).

Because of differences between *Swietenia* and *Brosimum* in their physiological characteristics, we expected the following results in a root trenching experiment conducted across a gradient in canopy-openness (see Coomes and Grubb 2000, Ricard *et al.* 2003). First, we predicted a greater response by *Swietenia* because of its greater physiological and morphological plasticity. Second, we expected that *Swietenia*'s response to trenching would increase with increasing canopy openness but that an effect would also be present below a closed canopy. We expected a trenching effect below a closed canopy because of the ability of *Swietenia* seedlings to respond to the higher

light, soil moisture, and nutrient levels that have been found in other forests during transitions between wet and dry seasons (Cuevas 1995, Coomes and Grubb 2000, Barberis and Tanner 2005).

MATERIALS AND METHODS

Study site

The study was conducted on the 20,000 ha community-owned and managed forest owned by the Ejido Noh Bec in southern Quintana Roo on the Yucatan Peninsula (19° 7' N, 88° 20' W). In recent decades, the dry season has extended from November through April (months with average precipitation <100 mm) with a total yearly rainfall of approximately 1500 mm (Snook 1993). Evergreen trees account for more of the basal area than dry-season deciduous trees (Pennington and Sarukhan 1968, Dickinson 1998). Emergent canopy trees reach about 30 m (Snook 1993).

Heavy clay soils in the upland study area were derived from limestone parent material (see Cuanalo de la Cerda 1964, Furley and Newey 1979). Although there is limited topographic relief, soil depth varies markedly with small changes in elevation and rocks are often exposed on upper portions of the topography. Soils are considered to be of moderate fertility (Simmons *et al.* 1959, Gretzinger 1994).

The trenching treatments were initiated during the 1993 wet season (August) over 100 ha of the area selectively logged during the dry season of 1992. Mean intensity of selective logging ranged from 1-3 m³ ha⁻¹ (i.e., the volume of wood harvested per hectare) with a mean felling gap size of 74 m² (maximum = 342 m²) (Dickinson *et al.* 2000b). The understory was impacted to varying degrees by the felling of large trees and the action of rubber-tired skidders used to drag logs of felled trees to concentrating yards (*bacadillas*).

Fine root distribution

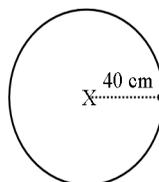
As a means of better understanding fine root distributions, we characterized fine root abundances in sites with contrasting soil depth. We sampled root-length densities (i.e., length of roots ≤ 2 mm diameter per unit volume of soil; Newman 1966) in soil pits in the upper 60 cm of a deep soil and over the entire soil profile in a shallow soil (down to 70 cm in pockets of soil and unconsolidated parent material).

Trenching experiment

To increase availability of soil-resources, we cut roots around target seedlings (i.e., the trenching treatment) and compared the effects of trenching with a treatment that controlled for the associated soil disturbance. Trenching has been the most common means of manipulating soil resource levels in studies of this type (Coomes and Grubb 2000) and has been shown to increase soil moisture (see, e.g., Horn 1985; Putz and Canham 1992; Gerhardt 1996a, 1996b) nutrient supply rates (Putz and Canham 1992, cf. Gerhardt 1996a) and reduce the fine-root biomass of potential competitors (Denslow *et al.* 1991, Gerwing 1995).

We applied the trenching and control treatments around naturally established seedlings of *Swietenia* (11-72 cm tall, mean height = 27 cm) and *Brosimum* (7-68 cm tall, mean height = 28 cm) over a range in canopy openness levels from closed canopy to one-year-old logging gaps (described below). We used *in situ* seedlings to avoid potential problem associated with abnormal root-system development in transplanted seedlings. We applied the control treatment to 78 and 44 seedlings and the trenching treatment to 76 and 43 seedlings of *Swietenia* and *Brosimum*, respectively. The treatments were applied alternately, without bias, as seedlings were encountered in stratified-randomly selected gaps and adjacent closed-canopy sites. In the trenching treatment, we cut all roots in a 20 to 30 cm deep circular trench 40 cm from each seedling (see Figure 1). We determined in a preliminary study that a trench with a 40 cm radius would have a large impact

Trenching treatment:
total length 126 cm



Control treatment:
total length 150 cm

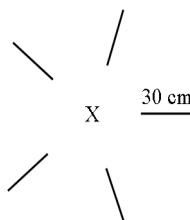


FIG 1. Diagram of the trenching and control treatments. Total trench length in the trenching treatment was 126 cm and in the control treatment was 150 cm.

on fine roots of potential competitors and little impact on the lateral roots of target seedlings. Trenching was done with a 12 kg bar with a sharp 5 cm wide blade at one end. The control treatment consisted of 5, 30-cm-long, trenches starting 30 cm from the base of each seedling and radiating away. The control trenches cut few roots of the target seedlings while causing similar levels of soil disturbance. The trenches were backfilled and the process was repeated each time that we measured the seedlings.

Seedling measurements

Stem length, stem diameter, and number of leaves (leaflets within compound leaves for *Swietenia*) were measured on each seedling in August 1993, February 1994, June 1994, and February 1995 (spanning one half of the first wet season, a dry season, and the entire second wet season). Stem length was measured to the nearest centimeter from the base of each seedling along the stem to its uppermost live meristem. Calipers were used to measure stem diameter at 10 cm above the base to the nearest

0.1 millimeter.

Soil depth and canopy openness

We measured soil depth with a 1 cm diameter iron bar 20 cm from each target seedling. Soil depth was measured either to the parent material or to 1.5 m. If bed rock was exposed where the measurement was made, soil depth was considered to be zero, even though the seedling itself was in a soil pocket.

Canopy openness was measured with a spherical densiometer (convex model, Lemmon 1956) at the height of the tallest leaf on each seedling on three occasions (August 1993, February 1994, and February 1995). In all analyses, we used a weighted average of the dry (February) and wet season measurements (August). To obtain the weighted average, the dry season measurements were averaged and weighted by 9/19 (months/month), the proportion of the experimental period that was dry season (historical average of <100 mm rainfall, see above). The wet season measurement was weighted by 10/19, the proportion of the experimental period that fell in the wet season. These weighted values were then summed. Our data do not allow us to account for any increases in shading in the logging disturbances through the experiment, but we expect any bias to be small because the experiment was of relatively short duration.

Analysis of seedling growth

We used the restricted maximum likelihood approach in SAS PROC MIXED (Littell et al. 1996) to analyze the effects of trenching, sample period, and covariates on relative growth with trenching and sample period (time) as fixed effects in the model. Soil depth and canopy openness were included as covariates. We modeled the correlation between time periods using several different correlation covariance structures and found that the first-order autoregressive structure resulted in the lowest AICC and BIC values in the majority of model runs. To determine whether to include a

covariate in a final model, we first determined whether the covariate was significantly related to relative growth (Littell *et al.* 1996). If so, the covariate and the covariate by treatment interaction term were included in a model and one or both were kept in the final model if their individual effect was significant. This selection process was repeated separately for each covariate.

Treatment (trenching or control) was applied at random to replicates (seedlings) and, within each replicate, estimates of stem length, diameter, and number of leaves (count + 1) were repeated on four occasions (see above). Relative growth rates (day^{-1}) were calculated as the difference between natural-log transformed measurements made at the beginning and end of each sample interval divided by the number of days between measurements. Although the lengths of sample intervals vary, conclusions about differences among sampling intervals drawn from repeated measures analyses are valid because relative growth rates are standardized by the length of the sample period. Number of leaves is a discrete variable, but its relative growth is nearly continuous, justifying the use of PROC MIXED. Values of canopy openness and soil depth (soil depth + 1) were natural-log transformed to improve linearity of relationships and homogeneity of variances.

Relative growth rate estimates with either large residuals or emergent influence (Cook's D values that were more than twice the size of others) or both and that caused unstable results were removed from some analyses. An unstable result was defined as a change in significance of one or more terms in an analysis when a high influence observation was added or removed. Separate assessments were made for each response variable (relative growth in stem, diameter, and number of leaves) resulting in the removal of 1-2 outliers for *Swietenia* and 1-3 for *Brosimum*.

In order to determine whether there was any initial bias in seedling stem length, diameter, and number of leaves related to trenching treatment, canopy openness, or soil depth, we related seedling measurements from the first sampling

event to these variables. Trenching and control treatments were compared with one-way analyses of variance. The relationships between seedling measurements and canopy openness and soil depth were determined with univariate regression. Species were analyzed separately and all continuous variables were natural-log transformed to linearize relationships and improve homogeneity of variances.

Seedling survival

We determined seedling mortality on each sampling date. Multiple logistic regressions were used in conjunction with likelihood-ratio tests (SAS Institute Inc. 1995) to determine the effect of species, trenching treatment, canopy openness, and soil depth on seedling survival. Canopy openness and soil depth were natural-log transformed to increase the evenness of their frequency distributions. Because species responded so differently to canopy openness, separate logistic regression analyses were conducted for each species.

RESULTS

Fine root distribution

Fifty-four percent and 45% of the total fine root-length density occurred in the upper 20 cm of soil in the deep and shallow soil, respectively (Table 1). The percentages of total

TABLE 1. Fine root density by layer in a shallow and deep soil. Density is quantified as the length of fine roots (<2 mm diameter) per volume of soil (cm cm⁻³). The depth to parent material was always greater than 60 cm in the deep soil while the entire soil profile was sampled in the shallow soil (including soil pockets that were up to 70 cm in depth). Surface soil was defined as that layer within 20 cm of the surface. The proportion of root-length density present in the surface layer is given in parentheses.

Soil	Root length density		
	N	Surface	Sub-surface
Shallow	6	2.6 (0.54)	1.2
Deep	6	1.7 (0.45)	0.7

root-length density in the upper 20 cm of soil are overestimated given that fine roots certainly occurred both below 60 cm in the deep soil area and within the parent material in the shallow soil area.

Initial relationships among variables

The initial measurements of stem length, diameter, and number of leaves were all positively correlated (data not shown). The correlations between these size-related variables were stronger for *Swietenia* (range in Pearson correlation coefficient: 0.75-0.81) than for *Brosimum* (range: 0.48-0.68). *Swietenia* seedling stem length and diameter and number of leaves were all positively related to canopy openness ($P < 0.001$) meaning that any effect of the trenching treatment must be interpreted cautiously. There were no significant relationships either between *Brosimum* initial seedling measurements and canopy openness ($P > 0.24$) or between initial measurements and soil depth for either species ($P > 0.33$). For both species, canopy openness values ranged from 1.6 to 62.8% (mean = 16.9, median = 14.0, $n = 235$) while soil depth ranged from 0 to 150 cm (mean = 41, median = 27, $n = 235$). There was no relationship between initial seedling size and trenching treatment ($P > 0.20$).

Seedling relative growth

Trenching resulted in significant increases in *Swietenia* relative stem length and diameter growth (Figure 2, Table 2) but contrary to hypothesis, trenching did not increase significantly as light levels increased, though relative growth rates of both trenched and control seedlings increased with light availability independently of the trenching treatment (Figure 3). Relative increase in number of leaves was greatest for trenched *Swietenia* seedlings and seedlings in the deepest soils. Contrary to prediction there was no evidence of an increase in the trenching effect during the dry season (Table 2, Figure 2). However, significant differences in relative growth among sampling intervals were

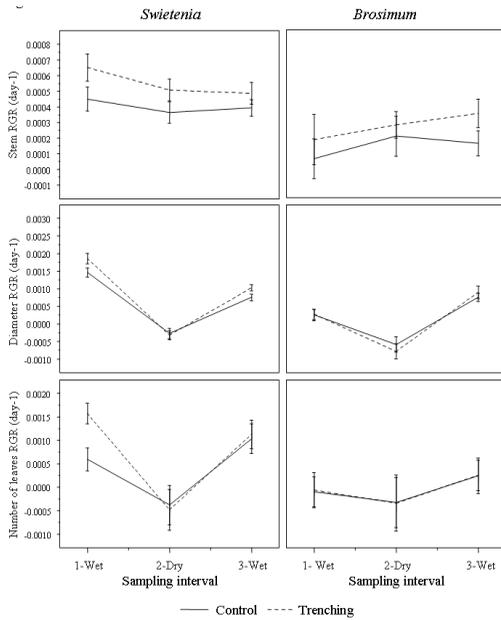


FIG 2. Average effects of trenching through time. Effect of trenching on *Swietenia* (left) and *Brosimum* (right) relative growth in stem length, number of leaves, and stem diameter (see Table 2). For *Swietenia*, the number of leaflets within compound leaves is given. Bars are ± 1 SE. Sampling interval 2 spanned a dry season, while intervals 1 and 3 included only wet season months. Outliers (see Figure 3) are not included in mean and standard error estimates.

evident for stem diameter and number of leaves, with stem diameter shrinkage and loss of leaves evident during the dry season (sample interval 2, Figure 2). We expected an effect of trenching on growth below a closed canopy for *Swietenia* (roughly 10% canopy openness or 2.3 on the log scale, Figure 3), however, no such effect was found.

As hypothesized, the trenching treatment had no effect on *Brosimum* growth across the canopy openness gradient (Figure 2, Table 2). There were also no effects of initial stem length, diameter, and number of leaves on response to trenching when these initial values were included as covariates. For *Brosimum* stem diameter relative growth, there was evidence for both differences among sampling intervals, with shrinkage during the dry season (sample interval 2, Figure 2), and for increases at higher light levels (Figure 3).

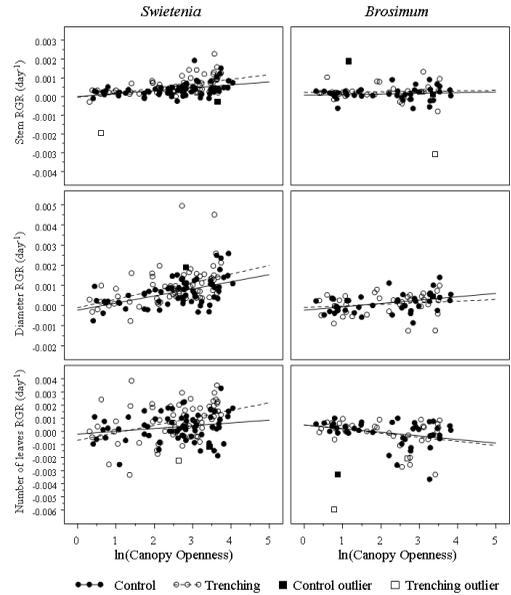


FIG 3. Effects of trenching over the canopy openness gradient. Average relative stem growth in trenching and control treatments over the experimental period for *Swietenia* (left) and *Brosimum* (right) seedlings is shown. Included in the averages are growth rates of seedlings that later died. Averages for seedlings that included one or more outlying relative growth rate estimates that were not used in statistical analyses are indicated on the plot.

Seedling survival

Swietenia seedling survival increased with increasing canopy openness (Table 3A). Survival at closed-canopy light levels (<10% canopy openness) was less for *Swietenia* than *Brosimum* whereas survival was the same for both species at gap light levels ($\geq 10\%$ canopy openness, Table 3B). No interactions between treatment, canopy openness, and soil depth were significant ($P > 0.05$) for either species. Accordingly, interactions were not included in the final logistic regression models (Table 3A).

DISCUSSION

Consistent with greater plasticity in physiological rates and resource allocation patterns, *Swietenia* seedling growth responded positively to the trenching treatment (Table 2), though the overall trenching effect was small (Figures 2 and 3). In contrast, trenching had no

TABLE 2. Mixed-model repeated-measures analyses of *Swietenia* (A) and *Brosimum* (B) relative growth in stem length, diameter, and number of leaves across the canopy openness gradient. Shown are the Type III tests of fixed effects. Canopy openness is the weighted average value over the experimental period, including wet and dry season measurements (see Methods). Only significant effects of depth and canopy openness and their interactions with trenching are shown.

A. SWIETENIA

Source	Numerator DF	Denominator DF	F	P
Stem length				
Trenching	1	57	5.56	0.0218
Time	2	227	2.59	0.0776
Trenching*Time	2	227	0.99	0.3717
Canopy	1	227	34.56	<0.0001
Stem diameter				
Trenching	1	58	4.94	0.0301
Time	2	227	131.76	<0.0001
Trenching*Time	2	227	2.06	0.1293
Canopy	1	227	54.73	<0.0001
Number of leaves				
Trenching	1	57	3.69	0.0599
Time	2	221	10.75	<0.0001
Trenching*Time	2	221	1.71	0.1836
Canopy	1	221	13.60	0.0003
Trenching*Depth	2	221	4.16	0.0169

B. BROSIMUM

Source	Numerator DF	Denominator DF	F	P
Stem length				
Trenching	1	32	2.28	0.1411
Time	2	134	0.74	0.4783
Trenching*Time	2	134	0.34	0.9103
Stem diameter				
Trenching	1	31	0.04	0.8353
Time	2	132	29.20	<0.0001
Trenching*Time	2	132	0.20	0.8214
Canopy	1	132	6.17	0.0142
Number of leaves				
Trenching	1	32	0.04	0.8388
Time	2	130	0.60	0.5498
Trenching*Time	2	130	0.02	0.9814

TABLE 3. Seedling survival over the experimental period. A. Likelihood ratio tests of the effects of trenching, canopy openness, and soil depth on *Swietenia* and *Brosimum* survival. Included are estimates of the slope parameters associated with a given variable in the multiple logistic regression equations (SAS Institute Inc. 1995). The slope parameters are interpreted as the slope of the relationship between a given variable in the regression equation and the probability of survival. For example, for *Swietenia*, the probability of surviving increases with canopy openness (the slope parameter is positive). The control treatment was coded as 0 and the trenching treatment as 1, thus, a positive slope would be interpreted as a positive effect of trenching. B. Frequency and percentage of seedlings of each species that survived or died over the experimental period at low and high canopy openness levels.

A.

Coefficient	Slope	df	Chi-Square	P
<i>Swietenia</i>				
Trenching	0.04	1	0.03	0.89
Canopy Openness	0.75	1	11.29	0.0008
Soil Depth	0.34	1	1.53	0.22
Trenching	0.37	1	1.40	0.24
Canopy Openness	-0.29	1	0.78	0.38
Soil Depth	-0.21	1	0.69	0.40

B.

Species	Alive	Dead
Low canopy openness (<10%)		
Chi-Square = 8.63, df = 1, P = 0.003.		
<i>Swietenia</i>	29(58.0)	21(42.0)
<i>Brosimum</i>	33(86.8)	5(13.2)
High canopy openness (>10%)		
Chi-Square = 1.05, df = 1, P = 0.31.		
<i>Swietenia</i>	80(86.0)	13(14.0)
<i>Brosimum</i>	34(79.1)	9(20.9)

effect on measurements of *Brosimum* seedling growth (Tables 2 and 3, Figure 3) and there were no effects of trenching on either *Swietenia* or *Brosimum* survival (Table 3A). In comparison with *Swietenia*, *Brosimum* is a species with less plasticity in physiological rates and biomass allocation to roots and shoots (Ramos and Grace 1990, Strauss-Debenedetti and Bazzaz 1991, Strauss-Debenedetti and Berlyn 1994) as well as

higher root-shoot ratios, thicker leaves (Ramos and Grace 1990), lower growth rates, and higher survival in closed-canopy conditions (Table 3B). These traits and deep taproots (see below) would be expected to result in a dampened response to trenching but would also allow *Brosimum* seedlings to persist in shaded conditions over long periods in which drought is a consistent risk (Coomes and Grubb 2000, Gerhardt and

Fredriksson 1995). Ability to persist at low light may be particularly beneficial in the study forest where periodic hurricanes are a dominant feature of the disturbance regime (Dickinson *et al.* 2000a; Snook 1993, 1996).

In combination, a lack of an effect of trenching on survival (Table 3A), the lack of a greater trenching effect during the dry season (Figure 2), and a positive relationship between soil depth and only one plant variable (relative increase in number of leaves for *Swietenia*, Table 2) suggest that the surface trenching treatment had a minimal effect on dry-season soil-resource availability for either species. This result is surprising considering that many seedlings encountered in the field occurred in microhabitats with minimal soil volume and, for both species, stem diameters decreased and seedlings lost leaves during the dry-season (Figure 2, see also Gerhardt 1996a). Variation in soils from shallow and rocky to deep (>2 m) over spatial scales of 10's to 100's of meters is a distinctive feature of Yucatan peninsula soils and shallow soils dry quickly (Cuanalo de la Cerda 1964, Furley and Newey 1979). Differences among seasons in the effect of trenching on *Swietenia* seedlings may have been reduced if trenching had affected both soil moisture and nutrient levels (e.g., Putz and Canham 1992) and those resources were limiting at different times of the year.

Various lines of evidence point to the importance of deep soil-moisture extraction (see also Gerhardt 1993, Gerhardt and Fredriksson 1995). Deep tap roots were the rule among seedlings we excavated in Noh Bec and tap roots in seedlings and trees have been shown to be crucial for the uptake of deep-soil moisture during seasonal drought (Gerhardt 1993, Cuevas 1995, Jackson *et al.* 1995). In Noh Bec, the vast majority of *Swietenia* and *Brosimum* seedlings excavated below a closed canopy had a well-defined taproot and this pattern was repeated in other species (see Dickinson 1998). Densities of fine roots in the upper 20 cm of the soil in this study were low (45- 55%, Table 1) compared to percentages reported in other seasonally-dry forests (see review in Cuevas 1995). Low

fine root densities in surface soils suggest that seedlings are exploiting moisture in both deep soil horizons and fissures in the limestone parent material. There was a consistent, though small, interaction between trenching and soil depth in their effect on relative increase in number of leaves for *Swietenia* suggesting that improved resource status on deep soils facilitated a response to surface trenching.

Increased seedling survival would have been expected for *Swietenia* in the trenching treatment because these seedlings, with increased growth, would have been more likely to develop a deeper tap root and thereby garner more dry-season soil moisture (Coomes and Grubb 2000, Gerhardt 1996a). In contrast to this expectation, there was no effect of trenching on *Swietenia* survival whether the seedlings were growing below the canopy or in gaps (Table 3A). In secondary forest with a rainfall regime similar to ours, Gerhardt (1996b) found that, for seedlings of several species (including *Swietenia*), the effect of trenching on survival below a closed canopy during the dry season was dependent on whether the canopy was partly deciduous, like at our study site, or completely deciduous. Trenching was only beneficial in the completely deciduous site, indicating an ameliorating effect of canopy cover during the dry season. Though there was no effect of trenching on survival in our study, *Swietenia* seedling survival increased with canopy openness and was equal to that for *Brosimum* in gaps while *Brosimum* survival did not vary with canopy openness (Table 3A and B).

We expected root competition to be present below a closed canopy but to have the greatest effect in gaps, at least for *Swietenia* (Coomes and Grubb 2000, Barberis and Tanner 2005). In contrast, there was no significant interaction between trenching treatment and canopy openness in their effect on measures of *Swietenia* growth (Table 2). It appears that the interaction was not significant because of both a relatively small effect of trenching and the presence of a large amount of unexplained variation in relative growth rates. In contrast to our results, Gerhardt (1996a) found significant

effects of trenching on *Swietenia* growth in unthinned plots below both semi-evergreen and dry-season deciduous canopies. The trenching treatment used in Gerhardt's study almost certainly had greater effects on soil resources than did our treatments and light levels in these shorter-statured, secondary forests were likely to have been higher than those in our closed-canopy study sites (though our canopy-openness estimates cannot be compared with their light measurements).

Apart from a small overall effect of trenching, several reasons for a lack of a significantly greater effect at higher light levels are possible. First, *Swietenia* seedlings were larger in gaps at the beginning of the trenching experiment (see Results) and larger seedlings respond less to soil resource augmentation because of their deeper root systems and more favorable water status (Fisher *et al.* 1991, Gerhardt 1996a, Poorter and Hayashida-Oliver 2000). Second, root competition in logging gaps may have already been reduced by disturbance to vegetation caused by logging machinery (rubber-tired skidders, Dickinson *et al.* 2000b), a disturbance that did not affect seedlings growing at low canopy openess levels. Third, increased herbivory and a trend in increased leader dieback at high canopy openess levels for the *Swietenia* seedlings in this study may have dampened the effect of root cutting (Dickinson 1998). Incidence of shoot borer (*Hypsipyla*) injury in separate study on planted seedlings was found to increase with relative growth rates (Dickinson and Whigham 1999). A final possibility is that trenching did not ameliorate nutrient limitations.

Phosphorus availability limits seedling growth in many tropical forests (*e.g.*, Raaimakers and Lambers 1996, Lawrence 2003), including forests in the study region (Cecon *et al.* 2004), and this phosphorus limitation is often ameliorated by mycorrhizal associations (*e.g.*, Moyersoer *et al.* 1998, de Grandcourt *et al.* 2004). It seems possible that trenching would disrupt mycorrhizal associations, possibly contributing to the relatively minor response to trenching found in this study. However, in two studies of trenching effects on nutrient poor

tropical soils, phosphorus was not demonstrably limiting (Coomes and Grubb 1998, Lewis and Tanner 2000).

Different responses to root competition and canopy openess by *Swietenia* and *Brosimum* support the conclusion that these species would require different regeneration methods within a larger silvicultural system designed to maintain both species in selectively logged forests (see Dickinson *et al.* 2000b). *Swietenia* shows its greatest growth rates after existing canopy and subcanopy trees have been removed by fire or heavy machinery in log concentrating yards (Dickinson and Whigham 1999; Snook 1993, 1996) and reaches the canopy infrequently in the small felling gaps typically created by the selective logging practiced in the region (Dickinson and Whigham 1999, Dickinson *et al.* 2000b). The results of our study would suggest that while the primary cause is probably sub-optimal light levels in relatively small felling gaps, root competition is at least a secondary cause. The abundance of *Brosimum* in this forest appears to be largely a function of survival through hurricanes (*e.g.*, Universidad Autonoma Chapingo 2007) and the persistence and slow growth of seedlings and saplings below a closed canopy (Dickinson *et al.* 2000b; Snook 1993, 1996). Reduced impact logging methods designed to minimize injury to advanced regeneration and minimize canopy disturbance (Pinard *et al.* 1995) would appear to be beneficial for *Brosimum* populations but would do little for *Swietenia* regeneration (*e.g.*, Dickinson and Whigham 1999, Dickinson *et al.* 2000b, Snook 1996).

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