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Tree regeneration in felling and natural treefall disturbances in a semideciduous tropical forest in Mexico

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Abstract

Tree regeneration was compared among closed-canopy sites and 4–11-year old natural and felling gaps in a selectively logged semideciduous tropical forest in southeastern Mexico. Closed-canopy sites and gaps were selected stratified randomly. In addition, all large natural and felling gaps encountered were sampled. All stems ≤ 5 cm dbh were sampled in sets of 10 m² plots in closed-canopy sites and gaps. The origins of the 10 tallest stems in each gap were also determined. Rubber-tired skidder disturbance in felling gaps resulted in a fourfold increase in the relative abundances of a set of shade-intolerant species. The logging process also promoted root sprouting, primarily among shade-intolerant species, but also in several shade-tolerant species. Advance growth accounted for a higher proportion of tall stems in natural than felling gaps and most of these stems were of shade-tolerant species. The proportion of tall stems that originated from seeds or small seedlings at the time of gap formation was higher in felling than natural gaps and increased with canopy openness only in felling gaps. These stems were primarily from shade-intolerant species. A lack of response to canopy openness in natural gaps was likely a result of relatively low levels of understory and substrate disturbance coupled with the absence of large natural gaps with high canopy openness. The maintenance of shade-intolerant and tolerant timber species in this forest would appear to require, at minimum, the creation of large gaps with understory and substrate disturbance within a matrix of forest logged by single-tree selection methods in which understory damage was minimized. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Small-scale treefall gaps (natural gaps) are the prevailing natural canopy disturbance between large-scale disturbance events (hurricanes and fires, Snook, 1993, 1998) in the seasonally-dry tropical

forest described in this paper. Natural gaps form isolated holes in an otherwise continuous canopy and occur at low rates in this forest relative to wetter tropical forests not affected by large-scale disturbances (Whigham et al., 1999). Tree regeneration in natural disturbances can serve as a guide for the design of regeneration methods whose purpose is the promotion of early establishment, survival, and growth of desired tree species (Smith, 1986; Brokaw et al., 1998; Snook, 1998; Hartshorn, 1989, 1995). Regeneration methods are an integral component of silvicultural systems (e.g., Smith, 1986).

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In addition to natural gaps, fires, and hurricanes, highly selective logging causes canopy disturbance in forests over much of the Yucatan region (see Primack et al., 1998). During recent years in the study forest, 1–3 m³ ha⁻¹ of marketable species larger than a minimum diameter (35 or 55 cm depending on species) have been felled in different logging areas each year within a planned 25 year cutting cycle (Argüelles, 1991; Snook, 1993). These logging intensities are typical of the region (Argüelles, 1991; Whitman et al., 1997) and are very low in a global context (FAO, 1995). Low logging intensities typically result in single-tree felling gaps that are scattered throughout a logging area. After trees are felled they are dragged to roads and log landings by rubber-tired skidders. Along the resulting skid trails, there is understory and substrate disturbance but little canopy opening (Whitman et al., 1997). In logged forest, felling gaps are the closest disturbance analog to natural gaps.

Regeneration in natural and felling gaps should differ because different disturbance conditions occur in natural and felling gaps (Uhl and Vieira, 1989; Boot and Gullison, 1995). The process of felling a tree opens a canopy gap and disturbs the understory. After felling has occurred in the study forest, logs are attached to winch cables and dragged from the gap behind rubber-tired skidders (for effects of tracked skidders, see Jonkers, 1987; Holdsworth and Uhl, 1997). The skidding process damages understory vegetation (Whitman et al., 1997), disturbs the litter and soil, and increases the size of gaps (Johns et al., 1996). In contrast, in natural gaps, disturbance to the soil and litter is primarily caused by uprooting, a form of stem failure that is uncommon in the study site (Dickinson, 1998; Whigham et al., 1998).

Given smaller gap sizes and less understory and substrate disturbance, shade-tolerant species were expected to be relatively favored in natural gaps. In felling gaps, larger canopy openings (Brokaw, 1985a; Swaine and Whitmore, 1988) and higher levels of disturbance to the understory and substrate (Putz, 1983; Putz and Appanah, 1987; Holdsworth and Uhl, 1997) were expected to favor shade-intolerant species that colonize new gaps from seeds or small seedlings.

In this paper, we compare tree regeneration between natural and felling gaps focussing on the effects of skidder disturbance and canopy openness. Tree regeneration in felling gaps opened by low-intensity, selec-

tive logging has been studied to a limited extent in the Yucatan (Macario Mendoza, 1991; Roque Alamina, 1991; Whitman et al., 1997; Brokaw et al., 1998) and has been only informally compared with tree regeneration in natural gaps in other tropical forests. In light of the results, we discuss the disturbance conditions that would be required as a component of regional regeneration methods designed to maintain both shade-intolerant and tolerant species in logged forest.

2. Methods

2.1. Study site

The study forest, Noh Bec, is communally-owned and covers approximately 18,000 ha in the southern part of the state of Quintana Roo, Mexico (19°7'N, 88°20'W). The forest is part of the Maya Forest region that encompasses southeastern Mexico, Belize, and northern Guatemala (Primack et al., 1998). The forest is semideciduous (Pennington and Sarukhán, 1968) and has been classified as tropical dry forest in the Holdridge system (Whigham et al., 1990). Yearly average rainfall is about 1500 mm and the dry season (with <100 mm rainfall per month) runs from January through April (Snook, 1993). Clayey soils are derived from limestone parent material (Ferrusquia Villafranca, 1993).

The study site included six logging areas on the western side of Noh Bec (1984 and 1986–1990 coupes), sampling was conducted from May to August 1994. Forests in the region have a long history of human (Hernandez, 1951; Edwards, 1986) and natural disturbance (e.g., Snook, 1993). Highly selective logging, primarily for *Swietenia macrophylla* (mahogany), was done in the study site prior to the 1980's (Sociedad Civil de Productores Forestales de Quintana Roo, unpublished data). There was no anecdotal evidence of fire for the last half century in the study site and major hurricane disturbance last occurred in Noh Bec in 1955 (Snook, 1993).

2.2. Gap and closed-canopy site selection and description

Stratified-randomly selected natural gaps, felling gaps, and closed-canopy sites were sampled. In

addition, all large natural ($>100\text{ m}^2$) and felling gaps ($>150\text{ m}^2$) encountered were sampled. We used a 15 km long logging road that ran through the middle of the study area as a baseline for choosing gaps and closed-canopy sites. We randomly located points along this road and at each point established a single 500 m long transect perpendicular to the road. The side of the road (left or right) on which to run the transect was randomly determined. A single closed-canopy site, natural gap, and felling gap were then sampled on each transect. A randomly selected non-gap point along each transect determined the position of the closed-canopy site. The felling gap closest to another randomly selected point was also sampled. The natural gap was chosen in the same way as the felling gap, but natural gaps were uncommon and no suitable natural gaps were encountered within 200 m on either side of several transects. Based on a 1 km wide sampling corridor along the logging road, the area sampled was approximately 1500 ha.

We used a canopy gap definition derived from Brokaw (1982): a vertically projected hole in the canopy that was estimated to have extended down to an average height of 2 m above the forest floor at the time the gap was created. Gaps in this study would often have been considered closed by the strict Brokaw (1982) definition because of upward growth of understory stems. We estimated gap area from a scale drawing based on four measured radii and freehand drawing of irregular gap margins. Only gaps estimated in the field to be 20 m^2 or greater were sampled. We only used natural gaps if we estimated that gap age was within the range of ages of the felling gaps (4–11 years). Although experience with felling gaps of known age was helpful, there was uncertainty in the aging of natural gaps.

Canopy openness was measured in the center of each gap and closed-canopy site. We measured canopy openness with a spherical densiometer held at chest level (convex model, Lemmon, 1956). Regenerating vegetation that would not have affected the canopy openness measurement if it had been taken at the time of gap formation occasionally reduced canopy cover. In order to estimate initial conditions in gaps, these stems were disregarded when canopy openness measurements were made. Excluding these stems was straightforward because individual crowns were distinguishable in the densiometer's mirror.

Gap-making trees were defined as trees that contributed to canopy opening. For felling gaps, this included all trees cut for timber. For natural gaps, only trees $>30\text{ cm dbh}$ were included. It was usually possible to identify a gap-making tree from its growth form and wood and bark characteristics.

2.3. Regeneration in gaps and closed-canopy sites

Except for stems $>5\text{ cm dbh}$ in closed-canopy sites, all stems were enumerated in square 10 m^2 plots in closed-canopy sites, natural gaps, and felling gaps (Table 1). Taxonomic authorities for the species included in this paper are given in Appendix A. Five adjacent plots were sampled in each closed-canopy site. In most gaps, as many adjacent plots were sampled as would fit. In the largest gaps, 6–12 adjacent plots were sampled in a randomly chosen portion of the gap. Plots in felling gaps were classified by whether they had been disturbed by the skidding process. Stem damage and patterns of soil disturbance were used to identify damage caused by skidder traversal and winching. A plot was coded as skidder-disturbed even if only a corner had been affected.

We identified the tallest 10 stems $>1.5\text{ m}$ in height within the entire area of each canopy gap and measured their heights (see Table 1 for sample sizes). 44 canopy gaps (37%) had fewer than 10 stems $>1.5\text{ m}$ in height; most of these had nine stems. Tall stems were

Table 1
Number of gaps in which plot-based and tall stem samples were made in the southeastern Mexican study forest^a

| | CC | NG | FG |
|--------------------------|----|----|----|
| <i>Plot sample</i> | | | |
| Stratified random | 50 | 31 | 41 |
| Large | – | 5 | 7 |
| Total | 50 | 36 | 48 |
| <i>Tall stems sample</i> | | | |
| Stratified random | – | 43 | 61 |
| Large | – | 5 | 7 |
| Total | – | 48 | 68 |

^a Closed-canopy sites (CC), natural gaps (NG), and felling gaps (FG) were selected stratified randomly. Also, all the large gaps encountered were sampled. The tallest stems present in each gap were sampled in all gaps in which plots were sampled and in the additional stratified-randomly selected gaps.

classified as either new seedlings, undamaged advance regeneration, damaged stems, or root sprouts. New seedlings were the stems for which there was no evidence that they had been present before the gap event. The other categories were composed of stems, or sprouts from stems, that were judged to have been present before the canopy gap event (advance growth).

Undamaged advance regeneration consisted of stems that were present before the canopy gap was opened and that were not damaged during its creation. Evidence that a stem had grown for some time below a closed canopy included (1) an abrupt change in stem architecture or bark and lichen morphology between basal (pre-gap) and upper (post-gap) portions of the stem and (2) comparisons of stem characteristics with stems of the same species that had regrown from damage caused by the gap event and were thus known to have been present before the gap event.

Damaged stems recovered by basal growth or growth along the stem above the base (>10 cm above ground level). Basal recovery was predominantly from adventitious sprouts (coppice), often from the root collar. Recovery from above 10 cm height involved replacement of the original leading stem by either a new sprout or growth of existing branches. The damaged stem category included individuals that were large before the gap event but the majority were from stems <10 cm dbh whose crowns were below a closed canopy.

Root sprouts were stems that arose from roots away from the root collar. Root systems were partially excavated and it was generally possible to make an unambiguous determination of root-sprout origin.

2.4. *Species classification*

Because physiological and demographic data were available for only a few species in the region, we classified species as being either relatively shade-tolerant or -intolerant. Shade-intolerant species were defined as those (1) with a high proportion of stems that originated from new seedlings among the tallest stems in gaps, (2) with a low proportion of stems in the plot sample that were both >50 cm in height and below a closed canopy, and (3) which had higher stem densities in gaps relative to closed-canopy sites. In contrast, shade-tolerant species were defined as those (1) with a high proportion of stems that

originated from advance growth in gaps, (2) with a high proportion of stems both >50 cm in height and below a closed canopy, and (3) which showed little or no difference in stem densities between closed-canopy sites and gaps.

2.5. *Statistical analyses*

The canopy openness and areas of stratified-randomly selected natural and felling gaps were compared with one-way analyses of variance. Univariate regressions were used to determine whether gap area and canopy openness increased with number of gap-making trees. Canopy openness and gap area were natural-log transformed in these analyses to normalize frequency distributions and increase homogeneity of variances. Both stratified-randomly selected and large gaps were included. Systat (1992) was used for the above and all other analyses.

We determined the effects of skidder disturbance on regeneration by comparing proportions of all stems in the plot sample accounted for by either shade-intolerant or tolerant species among natural gaps and plots in logging gaps that were either disturbed or undisturbed by skidders. Only stratified-randomly selected gaps were included. The unit of replication was the gap; thus, data from all plots in each natural gap were pooled as were data from either the skidder-disturbed or undisturbed plots in each felling gap. Tukey's honestly significant difference method was used after one-way analyses of variance to compare means. In the analysis of shade-intolerant species, we excluded species that root-sprouted because, in the plot sample, we could not distinguish stems that arose from root sprouts from stems that arose from new seedlings.

We regressed the proportion of new seedlings within the tall stems sample against canopy openness with the expectation that their proportions would increase with canopy openness. Analyses were done separately for natural and felling gaps using data from both stratified-randomly selected and large gaps. For felling gaps, we performed a separate analysis to determine if the proportion of the tallest stems originating from new seedlings in gaps would be expected to increase in large gaps simply if the proportion of gap area disturbed by skidders increased with gap area and canopy openness. To test this hypothesis, the proportion of plots disturbed by skidders was included

as a second independent variable. Canopy openness was natural-log transformed to better satisfy the homogeneity of variance assumption of regression.

We further compared natural and felling gaps by the frequencies of stems that arose from different origins. A chi-square test was applied to data from the tall stems sample in stratified-randomly selected gaps.

To determine whether a given shade-tolerance class would be favored in either natural or felling gaps, we compared natural and felling gaps using the frequency of occurrence of shade-intolerant and tolerant species within the sample of tall stems. Frequency refers to the number of natural gaps (or felling gaps) in which a species was present divided by the total number of stratified-randomly selected natural gaps (or felling gaps) in the sample. These tall stems were assumed to be those most likely to occupy the future canopy. A one-way analysis of variance was used.

3. Results

3.1. Gap and closed-canopy site characteristics

Gap area and canopy openness were positively related (Fig. 1). Among stratified-randomly selected gaps felling gaps were larger than natural gaps ($F_{(1,102)} = 6.34$, $P = 0.013$) but had similar canopy-

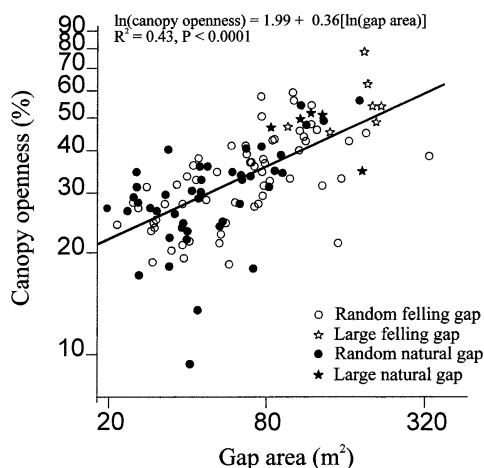


Fig. 1. Regression of canopy openness on area for canopy gaps in the southeastern Mexican study forest. Stratified-randomly selected gaps and all large gaps encountered are included (see key).

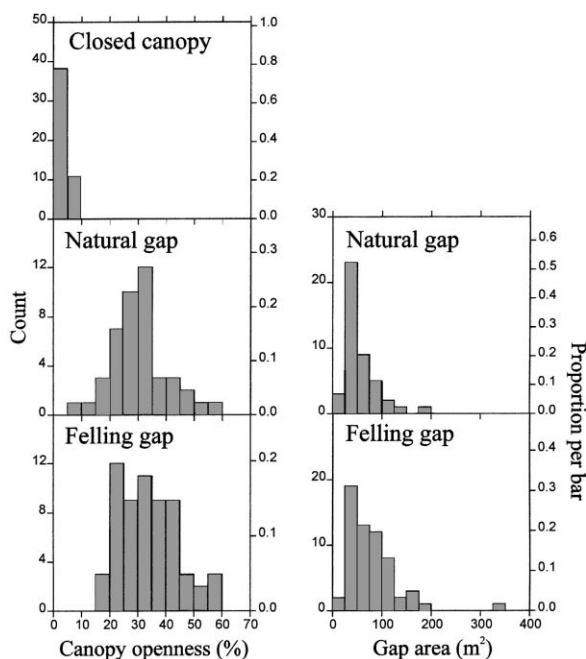


Fig. 2. Canopy openness (left) and gap area (right) for stratified-randomly selected gaps and closed-canopy sites in the southeastern Mexican study forest.

openness values ($F_{(1,102)} = 3.15$, $P = 0.079$, Fig. 2). The largest felling gaps were more open and larger than the most open and largest natural gaps in both the stratified-random and large gap samples (Fig. 1). Maximum gap sizes were 342 and 225 m² for felling and natural gaps, respectively. Closed-canopy sites had the lowest canopy openness values (Fig. 2).

The regression analysis indicated that gap area increased with number of gap-making trees in both natural ($R^2 = 0.29$, $P = 0.001$) and felling gaps ($R^2 = 0.12$, $P = 0.009$). Canopy openness also increased with number of gap-making trees in both natural ($R^2 = 0.07$, $P = 0.05$) and felling gaps ($R^2 = 0.14$, $P = 0.02$). Most natural (26 of 38, 68%) and felling gaps (46 of 57, 81%) were created by single gap-making trees.

Gap-maker identity differed considerably between natural and felling gaps (Fig. 3). Mahogany was the most heavily logged species while *Manilkara zapota* created the most natural gaps. Several species were both logged and created natural gaps.

40% of all plots in felling gaps were undisturbed by skidders, while 60% had some skidder disturbance.

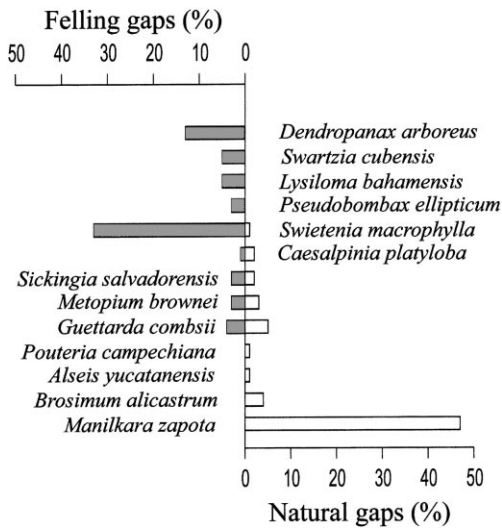


Fig. 3. The percentage of gap-making trees by species in felling (shaded bars, $n = 69$) and natural gaps (open bars, $n = 66$) in the southeastern Mexican study forest. Most gaps were created by one gap-making tree (see Section 3). Data from the stratified-random and large gap sample are pooled in the figure.

Because plots were coded as disturbed if only a corner was affected, 60% is an overestimate of overall skidder disturbance.

3.2. Species classification

Species for which there were sufficient data were classified as relatively shade tolerant or intolerant (Table 2). Except for one of the five sources for *Bursera simaruba*, all classifications were concordant with those from the literature. For a given classified species, the tallest stems of in canopy gaps originated predominantly from either undamaged advance regeneration or from new seedlings in gaps. For classification purposes, we pooled the sample of tall stems from natural gaps and felling gaps. Combining was justified given that species were highly consistent in their stem origins among gap types (Dickinson, 1998).

Out of the 821 stems that were classified by origin in gaps, shade-intolerant species (Table 3) accounted for more of the root-sprouts (9.5% of stems, 95% confidence interval 7.5–13.0%, Sokal and Sokal, 1995) than shade-tolerant species (1.0% of stems, 95% confidence interval 0.3–2.3%). Overall, 90.7% of root sprouts in the tall stem sample were from the shade-

intolerant species in Table 3. For purposes of this analysis, three species were tentatively classified (Table 2C); *Allophylus cominia* was very similar to species in the shade-intolerant species group while *Coccoloba spicata* and *Swartzia cubensis* exhibited characteristics of the shade-tolerant group.

3.3. Regeneration in natural and felling gaps

Nine shade-tolerant species' stems (Table 2) exhibited a fourfold reduction in their proportions among all stems in felling-gap plots disturbed by skidders relative to natural-gap plots and felling-gap plots undisturbed by skidders (Fig. 4, $F_{(2,74)} = 26.92$, $P < 0.0001$). In contrast, four shade-intolerant species (Table 2, those that were not found to root sprout: *Exostema mexicanum*, *Metopium brownei*, *Hampea trilobata*, *Cecropia obtusifolia*), showed a fourfold increase in their proportions in skidder-disturbed plots relative to natural-gap plots and felling-gap plots undisturbed by skidders (Fig. 4, $F_{(2,74)} = 13.36$, $P < 0.0001$).

The proportion of stems that originated from new seedlings in gaps increased with canopy openness in felling ($R^2 = 0.15$, $P = 0.0002$) but not natural gaps (Fig. 5, $R^2 < 0.01$, $P = 0.57$). For felling gaps, the result was significant even without large gaps ($R^2 = 0.20$, $P < 0.0001$). When the proportion of skidder-disturbed plots was included as an independent variable, its partial regression coefficient was not significant ($P = 0.84$). Canopy openness and proportion of disturbed plots were not correlated (Spearman rank coefficient = -0.16 , $P < 0.05$). Accordingly, the increase with canopy openness in the proportion of new seedlings in felling gaps appears to be attributable to canopy openness itself.

The origins of stems differed substantially between natural gaps and felling gaps (Fig. 6; chi-square = 147, $df = 3$, $P < 0.0001$). Root sprouts, which were almost exclusively a phenomenon of felling gaps, and the one coppice sprout from a felled tree were excluded from the analysis. There was proportionally much less undamaged advance regeneration, more basal regrowth, and more stems that had originated from new seedlings in felling gaps than in natural gaps. Overall, advance growth accounted for a greater percentage of stems in natural gaps than in felling gaps.

Table 2

Shade-tolerance classifications for species that were relatively common in the southeastern Mexican study forest^a

| Species | Stem origins (n) | | | Stems (>50 cm, %) | Stems ha ⁻¹ | | |
|--|------------------|-----|----|-------------------|------------------------|------|------|
| | NS | UAR | DS | | CC | NG | FG |
| A. Shade intolerant | | | | | | | |
| <i>Guettarda combsii</i> ^{b,c} | 135 | 1 | 13 | 0.3 | 20 | 504 | 3442 |
| <i>Dendropanax arboreus</i> ^{b,c,d} | 17 | 0 | 6 | 0 | 122 | 292 | 1066 |
| <i>Exostema mexicanum</i> | 10 | 0 | 2 | 1 | 28 | 226 | 1046 |
| <i>Bursera simaruba</i> ^{b,c,d,e,f} | 37 | 2 | 3 | 0 | 90 | 394 | 624 |
| <i>Metopium brownei</i> ^{f,g} | 16 | 0 | 2 | 0 | 53 | 219 | 812 |
| <i>Hampea trilobata</i> | 20 | 3 | 2 | 0 | 139 | 452 | 472 |
| <i>Cecropia obtusifolia</i> ^b | 22 | 0 | 0 | 0 | 0 | 190 | 234 |
| <i>Lysiloma bahamensis</i> | 9 | 0 | 0 | 0 | 0 | 0 | 228 |
| <i>Vitex gaumeri</i> ^{b,c} | 16 | 1 | 3 | 0 | 0 | 7 | 193 |
| B. Shade tolerant | | | | | | | |
| <i>Pouteria unilocularis</i> ^{b,c,h} | 6 | 73 | 47 | 22 | 19853 | 8744 | 5091 |
| <i>Nectandra salicifolia</i> ^c | 3 | 19 | 9 | 8 | 10926 | 9605 | 7111 |
| <i>Brosimum alicastrum</i> ^{b,c,g,h,i,j,k} | 2 | 12 | 31 | 3 | 4404 | 2190 | 706 |
| <i>Trichilia minutiflora</i> ^c | 0 | 12 | 37 | 12 | 3000 | 2752 | 1203 |
| <i>Drypetes lateriflora</i> | 0 | 7 | 10 | 4 | 1849 | 876 | 2051 |
| <i>Pithecellobium stevensonii</i> | 0 | 13 | 21 | 16 | 1469 | 1372 | 1411 |
| <i>Manilkara zapota</i> ^{b,c} | 0 | 19 | 9 | 13 | 1392 | 1540 | 700 |
| <i>Protium copal</i> ^{b,c} | 1 | 12 | 36 | 13 | 726 | 525 | 355 |
| <i>Pimenta dioica</i> | 1 | 9 | 15 | 9 | 257 | 255 | 96 |
| C. Relatively uncommon root-sprouting species | | | | | | | |
| <i>Allophylus cominia</i> | 9 | 2 | 8 | 0 | 200 | 460 | 640 |
| <i>Coccoloba spicata</i> | 1 | 3 | 27 | 25 | 110 | 51 | 193 |
| <i>Swartzia cubensis</i> | 0 | 4 | 10 | 5 | 114 | 88 | 269 |

^a The first three columns present the frequencies of stems in the tall stem sample that either arose from new seedlings (NS) or were present before the gap event and either were undamaged in the gap event (UAR) or were damaged and recovered (DS). The fourth column gives the percentage of stems below a closed canopy that were ≥ 50 cm in height (stems expected to have grown beyond their seed reserves). The final three columns are stem densities in 10 m² plots sampled in closed-canopy sites (CC) and natural (NG) and felling gaps (FG). Superscripts indicate sources for literature designations of shade tolerance. Root-sprouting species with relatively few stems in the tall stems sample are included at the bottom of the table to enable their tentative classification (see text and Table 3).

^b Negreros (1991).

^c Snook (1993).

^d Roque Alamina (1991).

^e Chavelas Polito and Devall (1988).

^f Sanchez Rejon (1994).

^g Oberbauer and Donnelly (1986).

^h Strauss-Debenedetti and Bazzaz (1991).

ⁱ Peters (1989).

^j Ramos and Grace (1990).

^k Welden et al. (1991).

Frequencies of shade-intolerant species were higher in felling than in natural gaps ($F_{(1,16)} = 19.4$, $P = 0.0004$, Fig. 7). The two species with the highest relative frequencies in felling gaps were species that root sprouted (*Guettarda combsii* and *Bursera simaruba*).

4. Discussion

Common shade-intolerant species were relatively favored in felling gaps (Fig. 7). This result can be attributed to increased regeneration from new seedlings where skidders traversed (Fig. 6), the larger

Table 3

Number and percentage of the tall stems in gaps that were root sprouts for the given species in the southeastern Mexican study forest^a

| Species | Number | Percentage |
|---|--------|------------|
| A. Shade intolerant | | |
| <i>Allophylus comini</i> ^b | 1 | 5 |
| <i>Alseis yucatanensis</i> ^c | 1 | 5 |
| <i>Bursera simaruba</i> | 6 | 12 |
| <i>Sickingia salvadorensis</i> ^c | 21 | 4 |
| <i>Dendropanax arboreus</i> | 29 | 56 |
| <i>Guettarda combsii</i> | 19 | 11 |
| <i>Vitex gaumeri</i> | 1 | 5 |
| B. Shade tolerant | | |
| <i>Brosimum alicastrum</i> | 1 | 2 |
| <i>Coccoloba spicata</i> ^b | 1 | 31 |
| <i>Swartzia cubensis</i> ^b | 6 | 30 |

^a Snook's classifications (Snook, 1993) are used for species for which there were too few stems in the tall stems sample to enable classification. Three relatively uncommon species are tentatively classified (Table 2C).

^b Tentative classification, see text and Table 2.

^c Classified by Snook (1993).

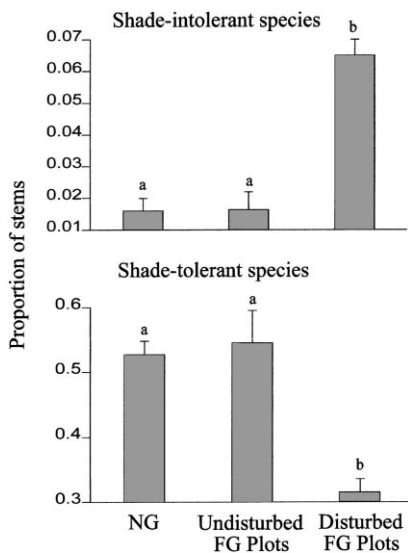


Fig. 4. Proportions of all stems accounted for by shade-intolerant and tolerant species (Table 2) in plots in the southeastern Mexican study forest. Bars represent natural gaps (NG, $n = 33$ gaps) and felling gap (FG) plots either undisturbed ($n = 11$ gaps) or disturbed by skidders ($n = 32$ gaps). Only stratified-randomly selected gaps are included. Shade-intolerant species which were found to root sprout are not included. Within each species group, a difference between mean proportions in a post-hoc comparison is indicated by a unique letter ($P < 0.05$).

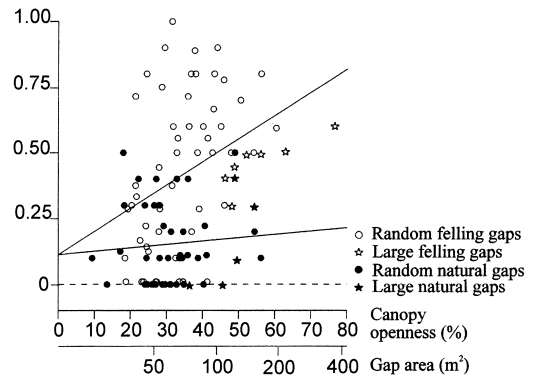


Fig. 5. Proportions of the tallest stems in gaps that originated from new seedlings as a function of canopy openness in natural and felling gaps in the southeastern Mexican study forest. Approximate area of these gaps is included for reference. Regression lines for felling and natural gaps are included (see text). The broken line represents gaps in which no stems originated from new seedlings and, along this line, the symbols for natural gaps are slightly offset for ease of comparison.

maximum size of felling gaps, and abundant root sprouting by several shade-intolerant species after logging (Table 3). In contrast, shade-tolerant species were relatively favored in natural gaps (Fig. 7). Relative abundances of shade-tolerant species were

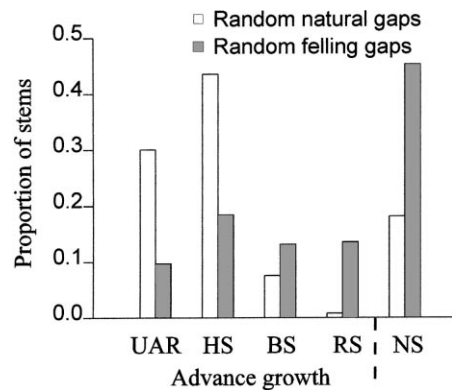


Fig. 6. Origins of the tallest stems in stratified-randomly selected natural ($n = 386$ stems) and felling ($n = 435$ stems) gaps in the southeastern Mexican study forest. Origins are undamaged advance regeneration (UAR), regrowth from ≥ 10 cm above the base on damaged stems ("high", HS), regrowth from < 10 cm above the base on damaged stems ("basal", BS), root sprouts (RS), and new seedling (NS). Regrowth from the base of damaged stems indicated severe damage and was generally coppice.

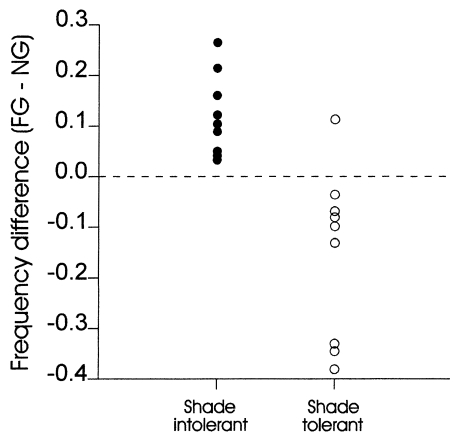


Fig. 7. Comparison between shade-intolerant and tolerant species (Table 2) in their frequencies in felling and natural gaps in the southeastern Mexican study forest. Frequency is based on presence or absence in the tall stems sample in a given gap. The average frequency of each species in natural gaps is subtracted from the species' frequency in felling gaps. Accordingly, the dotted line at zero indicates equal frequency in felling (FG) and natural gaps (NG). Only data from stratified-randomly selected gaps are included.

reduced by skidder disturbance (Fig. 4). In a northern Belizean forest logged with methods similar to those used in Noh Bec, 9% of saplings (>1.4 m high and <10 cm dbh) and 65% of trees (>10 cm dbh) were damaged in felling gaps during the logging process (Whitman et al., 1997). In Noh Bec, 60% of felling gap plots (10 m²) were at least partially disturbed by skidders.

By damaging understory stems, skidders extended the canopy gap (Brokaw, 1982) through the understory to ground level (Connell et al., 1997). Increased regeneration from new seedlings by shade-intolerant species in response to skidder disturbance may have involved a combination of decreased root and shoot competition from established vegetation along with increased disturbance to the soil and litter. Root competition in Noh Bec was experimentally shown to reduce growth of one shade-intolerant species in felling gaps (Dickinson, 1998). Negative competitive effects on colonizing seedlings by larger seedlings and pre-existing stems have been well documented in tropical felling gaps (Liew and Wong, 1973; Pinard et al., 1996; Kuusipalo et al., 1997), natural gaps (Brokaw, 1985b; Turner, 1990), and experimental

canopy gaps (Brown and Whitmore, 1992; Kennedy and Swaine, 1992).

Soil disturbance and litter removal have been described as key conditions for establishment from seed (Brandani et al., 1988; Raich and Christensen, 1989; Denslow, 1995; Grubb, 1996) and may also have contributed to the increased abundances of shade-intolerant species in felling gaps. Skidder traversal removed leaf litter over about 4% of felling gap area in Noh Bec (range 1–11%, $n = 8$, Dickinson, unpublished data). Soil disturbance from uprooted trees creates patches of bare soil and may also bring buried seeds to the surface (Putz, 1983; Putz and Appanah, 1987). Relative to wetter forests, soil disturbance from uprooting was an uncommon feature of natural gaps in the study site, only 18% of trees that fell in gaps were uproots (Dickinson, 1998; Whigham et al., 1999). A lack of uproots, and concomitant soil disturbance, may have contributed to the low abundances of shade-intolerant species in natural gaps.

As canopy openness increased, the proportion of stems that arose from new seedlings in felling gaps also increased (Fig. 5). Most of the stems were of shade-intolerant species. In felling gaps, this effect can be ascribed to increased canopy openness because the proportion of gap area disturbed by skidders did not increase with gap size. In contrast to felling gaps, in natural gaps, there was no relationship between the proportion of new seedlings among the tallest stems and canopy openness. Lack of a significant relationship in natural gaps was likely related to a combination of low levels of understory and substrate disturbance and a lack of large gaps with high canopy openness.

There was little overlap in gap-maker identity between natural gaps and felling gaps (Fig. 3). *Manilkara zapota* was by far the most frequent natural gap-making tree, while mahogany was the most heavily logged species. There was no evidence to suggest that differences between natural and felling gaps in gap-making tree identity affected the general results of the study. For instance, natural gap plots and felling gap plots undisturbed by skidders were indistinguishable in the relative abundances of shade-intolerant and intolerant species (Fig. 4), whereas, if propagule availability had been strongly related to gap-making tree identity, differences would have occurred.

Root-sprouting, primarily from shade-intolerant species, was caused by the logging process (Table 3). Compared with only 1% of the tallest stems in natural gaps, 13% of stems in felling gaps originated from root sprouts (Fig. 5). The mechanisms by which root-sprouting is caused for species in this region requires investigation before it will be possible to predict its occurrence. For several temperate species, mechanical damage to roots and the loss of apical dominance promote the formation of root sprouts (e.g., Schier, 1975; Schier and Campbell, 1978; Jones and Raynal, 1986, 1987, 1988). High levels of root-sprouting in felling gaps in this study may also be related to the fact that a higher proportion of root-sprouting species were logged than created natural gaps. Root-sprouts in felling gaps may out-compete seedlings just as seedlings are suppressed by advance growth (Pinard et al., 1996).

Damaged stems recovered by adventitious sprouts or from the growth of existing branches. Most of the tall stems damaged during gap events in this study were subcanopy stems and, consequently, shade-intolerant species were not commonly represented. Adventitious sprouting from damaged stems (coppice) was not separated from recovery by existing branches, but most regrowth from the base of stems among tall stems in gaps was coppice (Fig. 6, Dickinson, personal observation). Basal regrowth was more prevalent in felling than natural gaps, reflecting the often severe and extensive damage occasioned by skidders. Many of the species in Table 2, both shade intolerant and tolerant, have been reported to coppice abundantly after fire or thinning operations (Negreros, 1991; Snook, 1993). Only a single coppice from a felled, shade-intolerant tree (*Dendropanax arboreus*) occurred among the tallest stems in gaps; more such stems might have resulted if the felled trees had been of smaller diameters as in Negreros (1991).

Adventitious sprouting from roots and stems is an important pathway of response to disturbance in many dry-forest ecosystems (Ewel, 1977). Though most root sprouts were from shade-intolerant species, several shade-tolerant species were also represented (Table 3). As a consequence of recovery from damage, frequencies of several shade-tolerant species were similar in natural and logging gaps (Fig. 7). The importance of adventitious sprouting indicates that predicting regen-

eration response to disturbance requires more than information on shade tolerance.

4.1. Natural disturbance and regional regeneration methods

In the Yucatan, natural treefalls, hurricanes, and fires provide options in terms of natural disturbance models for regeneration methods. Though the most important timber species in southeastern Mexico are and have been shade intolerant (e.g., mahogany, *Dendropanax arboreus*, *Bursera simaruba*, *Metopium brownei*, and *Lysiloma bahamensis*), future logging is likely to increasingly target relatively abundant shade-tolerant species as more species are incorporated into the regional saw-timber market (e.g., *Brosimum alicastrum*, *Coccoloba spicata*, *Swartzia cubensis*, and, possibly, *Manilkara zapota*; Plumptre, 1990; Argüelles, 1991; Richards, 1991, 1993; Snook, 1993). Besides creating the proper disturbance conditions, regional regeneration methods will require attention to aspects of early tree establishment, growth, and survival not covered in this paper (Smith, 1986). For instance, evidence suggests that propagule availability constrains regeneration rates in the study site (Dickinson and Whigham, 1999).

Relative to disturbance created by the felling process, common shade-tolerant species were favored by natural treefall disturbance in this study (Fig. 7). Natural gaps, wherein opening of the canopy is accompanied by relatively low levels of understory and substrate disturbance, appear to provide a useful disturbance model for a regeneration method for shade-tolerant species. Relative to disturbances created by fire, shade-tolerant species were favored after hurricane disturbance in the study site, apparently also because of lower rates of damage to advance regeneration (Snook, 1993). Levels of understory damage in felling gaps could be minimized through the use of reduced-impact logging methods (e.g., Pinard et al., 1995; Johns et al., 1996; Bertault and Sist, 1997). Shade-tolerant timber species that recover effectively from coppice (e.g., *Brosimum alicastrum*; Negreros, 1991; Dickinson, personal observation) or root sprouts (e.g., *Coccoloba spicata* and *Swartzia cubensis*, Table 3) are expected to be least sensitive to the understory disturbance in felling gaps.

A regeneration method for shade-intolerant species that regenerate primarily from seed in canopy disturbances would appear, from this study, to require relatively large canopy openings in which there was disturbance to the understory and substrate (see also Brokaw et al., 1998). Severe understory and substrate disturbance that removes sources of adventitious sprouts and prepares a seed bed have been recommended and are being tested as a means of promoting mahogany regeneration (Brokaw et al., 1998; Snook, 1998). These disturbance conditions appear to mimic those created by intense fires and may be adequately reproduced by bulldozer clearings (Brokaw et al., 1998) and slash and burn agriculture (Snook, 1998). How much canopy opening and understory and substrate disturbance is required for adequate regeneration from seed by shade-intolerant species has yet to be determined (see Brokaw et al., 1998; Dickinson and Whigham, 1999) and whether species differ significantly in their requirements is not known.

In logged forest, regeneration of shade-intolerant timber species that root sprout (e.g., *Dendropanax arboreus* and *Bursera simaruba*, Table 3) or coppice might not be as tied to sites with high levels of understory and substrate disturbance as species that regenerate predominantly from new seedlings in gaps. Furthermore, the high levels of adventitious sprouting i.e., root sprouting and coppicing seen in felling disturbances by certain shade-intolerant species (e.g., Table 3) suggests that active management of adventitious sprouting may be a necessary and useful component of regeneration methods in this forest, particularly if regeneration from seed in felling gaps and other logging disturbances is uncommon.

As for temperate shade-intolerant species (e.g., Spurr and Barnes, 1973; Murphy et al., 1993; Johnson, 1993), selective logging regimes have been found to result in inadequate regeneration of mahogany (Snook, 1996; Dickinson and Whigham, 1999). Evidence from this study suggests that regeneration of shade-intolerant timber species would be disfavored to the extent that the felling process mimics natural treefalls. Like natural gaps, most felling gaps are small in this forest (Fig. 2). This fact coupled with the increase in proportions of shade-intolerant species with felling gap size indicates that regeneration rates of shade-intolerant species are limited by a lack of large felling gaps. The cost-effective creation of large

gaps with associated understory and substrate disturbance would be facilitated by the group felling of mature trees. The ability to create adequate numbers of multiple-tree gaps through felling alone is currently limited by a lack of markets for several relatively abundant, potential timber species (Plumptre, 1990).

The dichotomy in regeneration behavior between common shade-intolerant and tolerant species suggests that at least two regeneration methods must be practised on the same land base if the abundances of species in both groups are to be maintained (Stanley and Gretzinger, 1996; Pinard et al., 1999). To achieve such a goal in a dry tropical forest in Bolivia, Pinard et al. (1999) suggested a mixed silvicultural system that would result in the occurrence of even-aged groups of primarily shade-intolerant species within an uneven-aged matrix of primarily shade-tolerant species (see Nyland, 1996). In southeastern Mexico, such a spatial pattern of age distributions and species composition might be accomplished by the creation of large canopy gaps with understory and substrate disturbance within a matrix of forest logged by single-tree selection methods in which disturbance to the understory were minimized. Within this framework, attention to conditions that promote coppice and root sprouting may also be required.

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Appendix A.

Taxonomic authorities, families, and common names of species included in the paper.

| Species | Family | Common name | Source |
|--|---------------|--------------------------|--------------------------------|
| <i>Allophylus cominia</i> (L.) Sw. | Sapindaceae | Chachalaquillo | Standley (1930) |
| <i>Alseï yucatanensis</i> Standl. | Rubiaceae | Tabaquillo | Pennington and Sarukhán (1968) |
| <i>Brosimum alicastrum</i> Sw. | Moraceae | Ramon | Pennington and Sarukhán (1968) |
| <i>Bursera simaruba</i> (L.) Sarg. | Burseraceae | Chaca roja | Pennington and Sarukhán (1968) |
| <i>Caesalpinia platyloba</i> Wats. (= <i>C. violaceae</i>) | Leguminosae | Chacteviga | Standley (1930) |
| <i>Cecropia obtusifolia</i> L. (= <i>C. peltata</i>) | Moraceae | Guarumbo | Pennington and Sarukhán (1968) |
| <i>Coccoloba spicata</i> Lundell | Polygonaceae | Boop | Hawthorne and Hughes (1996) |
| <i>Dendropanax arboreus</i> (L.) Planch. & Decne. | Araliaceae | Sac-chaca | Pennington and Sarukhán (1968) |
| <i>Drypetes lateriflora</i> (Sw.) Krug. & Urb. | Euphorbiaceae | Kekenche, palo de puerco | Standley (1930) |
| <i>Exostema mexicanum</i> Gray | Rubiaceae | Malacate | Standley (1930) |
| <i>Guettarda combsii</i> Urb. | Rubiaceae | Tastap, verde lucero | Hawthorne and Hughes (1996) |
| <i>Hampea trilobata</i> Standl. | Bombacaceae | Mahahua | Standley (1930) |
| <i>Lysiloma bahamensis</i> Benth. (= <i>L. latisiliqua</i>) | Leguminosae | Dzalam | Pennington and Sarukhán (1968) |
| <i>Manilkara zapota</i> (L.) v. Royen | Sapotaceae | Chicozapote | Pennington and Sarukhán (1968) |
| <i>Metopium brownei</i> (Jacq.) Urb. | Anacardiaceae | Chechem negro | Pennington and Sarukhán (1968) |
| <i>Nectranda salicifolia</i> (Sw.) Griseb. (= <i>N. coriacea</i>) | Lauraceae | Laurel | Hawthorne and Hughes (1996) |
| <i>Pimenta dioica</i> (L.) Merrill | Myrtaceae | Pimienta | Pennington and Sarukhán (1968) |
| <i>Pithecellobium stevensonii</i> | Leguminosae | Chilillo | |
| <i>Pouteria campechiana</i> (Kunth) Baehni | Sapotaceae | K'anixte | Pennington and Sarukhán (1968) |
| <i>Pouteria unilocularis</i> (Donn. Sm.) Baehni | Sapotaceae | Zapotillo | Pennington and Sarukhán (1968) |
| <i>Protium copal</i> (Schlecht. & Cham.) Engl. | Burseraceae | Copal | Pennington and Sarukhán (1968) |
| <i>Pseudobombax ellipticum</i> (Kunth) Dugand | Bombacaceae | Amapola | Pennington and Sarukhán (1968) |
| <i>Sickingia salvadorensis</i> Standl. (= <i>Cosmocalys spectabilis</i>) | Rubiaceae | Chakte-kok | Standley (1930) |

(Continued)

| Species | Family | Common name | Source |
|---|-------------|-----------------|--------------------------------|
| <i>Swartzia cubensis</i> (Britt. & Wilson) Standl. | Leguminosae | K'atalox | Pennington and Sarukhán (1968) |
| <i>Swietenia macrophylla</i> King | Meliaceae | Caoba, mahogany | Pennington and Sarukhán (1968) |
| <i>Trichilia minutiflora</i> Standl. | Meliaceae | Limonaria | Standley (1930) |
| <i>Vitex gaumeri</i> Greenm. | Verbenaceae | Yaaxnik | Standley (1930) |

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