

ASSESSING TRADE-OFFS IN MULTIPLE-OBJECTIVE TROPICAL FOREST
MANAGEMENT

By

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Geoffrey Michael Blate

This document is dedicated to my father, who I wish I could have known, and to my mother, who raised me with tremendous courage and unconditional love after his death. It is also dedicated to my late mother-in-law, who very much wanted to celebrate its completion with me.

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While tropical forests continue to be cleared at alarming rates, the debate over how best to conserve them often proceeds without a clear understanding of the trade-offs that result from different management alternatives. Because timber is the most valuable product of tropical forests, substantial effort has been directed to harmonizing timber production and other goals, especially carbon sequestration and biodiversity conservation. Unfortunately, the nature and magnitude of the trade-offs between timber production and these objectives remain unclear and depend on numerous factors. By elucidating the key biophysical factors that influence forest management trade-offs, I aimed to better inform the quest to manage tropical forests for multiple benefits.

I assessed the trade-offs between timber production and fire susceptibility in a seasonally dry forest in lowland Bolivia subjected to four silvicultural treatments of increasing intensity aimed at achieving sustained timber yields (STY). By quantifying treatment effects on fuel loads, vegetative cover, dry-down rates of 10-h fuels, and fire

spread, I found that the treatments had little effect on fire susceptibility; this forest is fire-prone for about 130 days per year, even in the absence of logging. Fire severity, however, would likely be greater with intensive management due to increases in 1,000-h fuels.

Using a simulation model (SYMFOR) to project the effects of the silvicultural treatments on future timber yields, forest structure and composition, and biomass, I found that none of the treatments came close to achieving STY, indicating that silviculture would probably need to be intensified to secure STY. Neither forest structure nor species composition changed appreciably over two cutting cycles (60 years) in any of the treatments.

By contrasting the Bolivian forest with eastern Amazon and Borneo forests, I found that the trade-offs resulting from intensive silviculture to secure STY paled in comparison to the loss of forests. If maintenance of productive forest for both timber and carbon with a full complement of biodiversity is the goal, then fire (and not silviculture) is the menace. Fire prevention must complement silvicultural treatments to achieve sustained yields if tropical forests are to serve both production and conservation goals.

CHAPTER 1
MODEST TRADE-OFFS BETWEEN TIMBER MANAGEMENT AND FIRE
SUSCEPTIBILITY IN A BOLIVIAN SEMI-DECIDUOUS FOREST

Introduction

Forest managers have long recognized that not all forest uses or objectives can be simultaneously maximized (Dana 1943, Toman and Ashton 1996). Despite this realization, sustainable forest management (which promises continuous delivery and maintenance of multiple goods, services, and processes) has become the predominant management paradigm in tropical countries. Although research into the compatibility among different objectives of forest management has advanced substantially in temperate forests (Johnson et al. 2002, Stevens and Montgomery 2002), such research is scarce in tropical forests. Elucidating management trade-offs between sustained timber production and fire susceptibility is especially important considering the large proportion of tropical forests designated for timber production, the potential for such forests to contribute to conservation and development objectives, and the increasing prevalence of wildfire in these forests.

Despite increasing attention to the problem of fires in tropical forests (Goldammer 1990, Nepstad et al. 2001, Cochrane 2003) and the recognized role of logging in exacerbating the fire problem (Woods 1989, Holdsworth and Uhl 1997, Nepstad et al. 1999a, Cochrane 2003) especially during El Niño-related droughts (Siegert et al. 2001), few studies have determined the extent to which increased fire susceptibility is an inevitable consequence of intensifying management to achieve silvicultural objectives.

Holdsworth and Uhl (1997) showed that fire susceptibility (i.e., likelihood of fires starting and spreading in a forest) decreases when logging impacts are reduced in eastern Amazonian evergreen forests, where deep roots help most trees retain their foliage during the marked dry season (Nepstad et al. 1995). Unfortunately, reducing logging damage will not sustain timber yields, let alone achieve sustainable forest management, in seasonally dry, semi-deciduous forests. These forests typically require post-harvest silvicultural treatments (e.g., liana cutting, felling gap enlargement, and soil scarification) to promote regeneration and growth of commercial tree species, many of which are shade intolerant and lack adequate regeneration (Mostacedo and Fredericksen 1999, Fredericksen and Mostacedo 2000, Fredericksen et al. 2003). Considering that seasonally dry tropical forests encompass more area and are more affected by people than wet forests (Mooney et al. 1995), it is important to understand whether the intensive management regimes thought necessary to sustain commercial timber species and hence prevent conversion to other land uses, might elevate fire susceptibility and inadvertently promote forest conversion. My study was conducted in a region of the Bolivian Amazon where forest management is hoped to provide an economically viable alternative to conversion of forests to pasture land, which has increased dramatically in recent decades (Steininger et al. 2001).

Studies throughout the tropics show that logging increases forest susceptibility to fire (Kauffman and Uhl 1990, Siegert et al. 2001, Cochrane 2003) as well as fire severity (i.e., fire behavior and its ecological effects; Kauffman 1991) because logging results in a drier understory and increased fuel loads (Uhl and Kauffman 1990). Because additional silvicultural treatments beyond harvesting probably exacerbate the factors that drive fire

susceptibility and influence fire severity, it seems reasonable to expect that intensively managed forests would be more prone to wildfires of greater severity than undisturbed or less-intensively managed forests. Moreover, because more radiation reaches the forest understory in deciduous forests, they are more likely to be fire-prone than are wetter, evergreen forests (Swaine 1992).

The purpose of my study was to elucidate the nature and extent of tradeoffs between sustaining commercial timber yields and increasing fire susceptibility in a semi-deciduous tropical forest, and to contrast these findings with published studies from moister sites. I expected that more intensive management would

- Increase the proportion of the forest that is fire-prone on any given day during the dry season;
- Extend the number of fire-prone days during the dry season;
- Increase the potential for severe or catastrophic fires; and,
- Increase the number of months or years of elevated fire susceptibility above background levels (i.e., compared to un-logged control areas).

Site Description

My study was conducted in a 100,000 ha Forest Stewardship Council-certified timber concession operated by Agroindustria Forestal La Chonta Ltda. in Guarayos Forest Reserve (15°45'S, 62°60'W) in the Bolivian lowlands (200–400 m.a.s.l.).

According to the Holdridge classification system, the concession (hereafter La Chonta) is covered by subtropical humid forest. Seasonally deciduous and semi-deciduous forests like La Chonta provide about 45% of Bolivia's timber, and encompass about 35% of its designated forest management area (Superintendencia Forestal 2001). Biomass estimates for the region are 73–190 Mg/ha (Dauber et al. 2000). Mean annual temperature is ~24.5°C and mean annual rainfall is ~1,500 mm, 77% of which falls between November

and April. During the peak of the fire season (July–September) in average years, only 43 mm of rain falls monthly and understory vapor pressure deficits range from 0.6 to 0.8 kPa. Soils are moderately fertile inceptisols, but 10 to 15% of the area has black anthrosols enriched by humans several hundred years ago (Paz 2003).

The fire history of the region is unknown, but evidence that people extensively inhabited much of La Chonta and the presence of charcoal in the subsoil (Paz 2003) both suggest that the forest was historically subjected to fire. In 1995, an escaped fire burned about 30% of the La Chonta concession (Pinard et al. 1999, Mostacedo et al. 2001, Gould et al. 2002), killing 23% of the trees (dbh > 10 cm) and 75% of the lianas, and causing a proliferation of herbaceous vines (Pinard et al. 1999). Commercial tree regeneration remained scarce 5 years after the fire (Gould et al. 2002). Another fire in 1999 nearly destroyed the town on La Chonta's southwest border, but did not otherwise affect the concession. These fires occurred between July and September, when people in the fragmented matrix of fire-maintained, anthropogenic palm savannas and active agricultural fields surrounding La Chonta set fires to clear woody vegetation.

La Chonta is situated in a transitional zone between wetter forests to the north and drier forests to the south and southeast, and is dominated by canopy tree species characteristic of humid forests including Ficus boliviana, Hura crepitans, and Pseudolmedia laevis. Tree species common in drier forests (e.g., Centrolobium microchaete, Chorisia speciosa, and Cedrela fissilis) are also present in La Chonta. Although only a few high-value timber species (e.g., Swietenia macrophylla and C. fissilis) were harvested between 1980 and the mid-1990s, 10–12 tree species were harvested during my study (2001 to 2003). About 7–20 m³/ha of wood (3–5 trees/ha)

were harvested from annual management units that each encompassed ~2,300 ha. Harvest activities are planned based on a 30-year cutting cycle and implemented in accordance with Forest Stewardship Council certification standards and criteria. Minimum diameter for felling set by law is 70 cm for H. crepitans and F. boliviana, and 50 cm for all other species. Approximately 20% of trees above the diameter limit are left as seed trees.

Methods

Design

My study was conducted in and near 27-ha permanent plots established as part of a long-term silvicultural research project (LTSRP, IBIF 2004). The LTSRP applied four treatments representing a range of management options and intensities: “control” = no logging; “normal logging” = planned logging with no other silviculture; “improved management” = “normal logging” with liberation of future-crop trees from vines and overtopping non-commercial trees; and, “intensive management” = “improved management” with double the harvest intensity, additional future-crop tree liberation, and soil scarification in selected felling gaps. The improved and intensive treatments aimed to promote the regeneration and growth of commercial timber species, most of which are light-demanding (Mostacedo and Fredericksen 1999, Pariona et al. 2003). Treatments were randomly applied to 27 ha plots in each block, which were situated in three different harvest units (3 blocks × 4 treatments = 12 plots).

My study was conducted in and near Blocks 2 (harvested between May and July 2001) and 3 (harvested between February and July 2002). Because roads can act as fire conduits (Dell 1970, Wilson 1979, Schwartz and Caro 2003), it is important to note that although skid trails were included, roads did not traverse the treatment plots. Although

the forest appeared disturbed, signs of previous fire were only evident in a few small patches of the intensive plot and no old stumps from previous logging entries were found in any of the plots.

Treatment Effects on Forest Structure and Vegetative Cover

To compare harvest treatment impacts on forest structure, I compared the harvest volumes and basal area removed, as well as the corresponding ground and crown area disturbed by harvest operations. Residual tree densities and basal areas were also compared, based on post-harvest censuses of the 3 harvest treatment plots and the control plot. To estimate the impacts of each treatment on vegetative cover, I measured cover at 5 m intervals along four transects (spaced 75 m apart) per treatment previously established in Block 2. The total number of sample points was 327 for the intensive treatment, 363 for the improved treatment, 338 for the normal treatment, and 377 for the control treatment. The transect lengths varied between 400 and 500 m depending on the distance from the southern to the northern border of each treatment plot. All cover estimates were made in early December 2001, by which time deciduous trees were in full leaf.

I estimated the percentage of vegetative cover in six vertical strata (0–1 m; 1–2 m; 2–4 m; 4–8 m; 8–16 m; and >16 m) by viewing upward through a clear grid of twenty-five 3 cm × 3 cm squares (Mostacedo and Fredericksen 2000). I counted the number of squares covered and half-covered with vegetation in each stratum. To increase the accuracy of ocular estimates of vertical heights, a 14 m telescopic pole was used for daily calibration. Where total cover is reported, it is shown as a percentage and is simply the sum of the six percentages of cover (one per stratum).

At each sample point, I also estimated the horizontal distance to the nearest gap (felling or natural) and classified each point by habitat type. I defined a gap as any area $\geq 10 \text{ m}^2$ in which the highest vegetation was $\leq 2 \text{ m}$ tall (Brokaw 1982). Habitat classes were

- Undisturbed;
- Felling gap;
- Felling gap edge (0–20 m from gap);
- Skid trail;
- Skid trail edge (0–20 m from edge);
- Natural gap; and,
- Natural gap edge (0–20 m from gap).

Means from each transect per treatment were used to test for treatment differences in a one-way ANOVA; separate tests were conducted for each cover stratum, total cover, and distance to gap. Because the 4 transects per treatment were all located in one block, they do not constitute true replicates. Nevertheless, inferential statistics were used to indicate whether cover differed by treatment (Oksanen 2001).

Treatment Effects on Fuel Loads

To assess treatment impacts on fuel loads, censuses were conducted 6 and 15 months post-harvest in Block 2 using the planar transect method (van Wagner 1968, Brown 1974, Uhl and Kauffman 1990). In each census, 36–47 randomly oriented transects were established starting at 50 m intervals in each treatment plot. Transects consisted of vertical planes (extending from the ground to 2.5 m) of variable length depending on the diameter of the woody debris, with planes 11 m long for 1,000-h fuels ($> 7.5 \text{ cm}$), 5 m long for 100-h fuels (2.5–7.5 cm), 2 m long for 10-h fuels (0.6–2.5 cm), and 1 m long for 1-h fuels ($< 0.6 \text{ cm}$). The fuel time-lag concept is based on observations that as relative humidity changes, fuel moisture changes in an exponential fashion; and

that smaller diameter fuels gain or lose moisture faster than larger diameter fuels, because of their higher surface area to volume ratio (Agee 1993).

Wood fragments of each size class were tallied if they crossed the sample plane. Separate tallies for 1,000-h fuels were made according to three decay classes (sound, intermediate, and rotten) described by Delaney et al. (1998). Calipers were used to measure diameters of all 1,000-h fuels and a sample of smaller woody debris to obtain mean diameters for those size classes. Leaf litter depth was measured at three points along each transect.

To obtain fuel-mass estimates, samples of litter and woody debris were collected from the transects. Litter samples (all 1-h fuels down to mineral soil) from quadrats (20×20 cm) located at the beginning of each transect were oven-dried at 80°C to constant weight. The first three pieces of 1-, 10-, and 100-h fuels were collected from each transect to determine average wood density for each size class. Random samples of larger pieces in each decay class were obtained elsewhere in each treatment plot.

Wood densities were calculated from measurements of the fresh volume (by water displacement) and the oven dry mass of each sample. Heartwood, sapwood, and bark were included in cases where large sections of trunk measured. Masses for each size class were computed on a tons per hectare basis as per methods described by Brown (1974) using the combined data from all transects within each treatment. To compare differences among treatments, the log-transformed values for each transect in each treatment were used in an ANOVA. Although the transects in each treatment did not constitute true replicates, the only way to objectively compare the effect of the treatments

on fuel loads was to use inferential statistics. Treatment impacts on leaf litter depth and litter mass were compared in a similar manner.

Vegetation Cover and Dry-Down Relationships

I determined the number of days needed to dry 10-h fuels to 12% moisture content under a range of canopy-cover conditions during the early and mid-dry season. Uhl and Kauffman (1990) considered 12% to be the threshold moisture content below which forest fuels could easily ignite. From 10–19 July 2001, I measured dry-down rates of 10-h fuel sticks made from a local species (H. crepitans), but otherwise identical to the standard pine fuel sticks (four 35-cm × 1-cm diameter dowels connected in a plane by small dowels and staples) used by other researchers (Uhl and Kauffman 1990, Holdsworth and Uhl 1997).

I placed 10 fuel sticks along each of 5 variable-length transects (50–75 m) that originated in the centers of logging gaps (50–250 m apart) and extended into undisturbed patches of forest in the intensive treatment plot of Block 2. After soaking overnight in water to simulate a substantial rainstorm, the fuel sticks were suspended ~25 cm above the forest floor, in a stratified random manner to represent the range of cover conditions present throughout the four management treatments; sticks within a transect were at least 5 m apart. I repeated this experiment in Block 3, in late May 2002, using standard pine sticks to determine the number of days necessary for 10-h fuels to reach 12% moisture content in the early dry season. For analyses, the moisture contents of the H. crepitans fuel sticks were adjusted to values for standard pine fuel sticks, based on regression of average moisture contents of both species during controlled drying ($R^2 = 0.98$).

Data collected included vegetative cover estimates, temperature, relative humidity, and moisture content of the fuel sticks. I estimated cover in six vertical strata above each

fuel stick, using the grid method described above. I recorded temperature and relative humidity at 2 hour intervals for 2 weeks in 8 of the sites, using Hobo® (Onset Computer Corporation, Bourne, MA) temperature / relative humidity data loggers. I calculated vapor pressure deficit as a function of mean maximum temperature and mean minimum relative humidity at 1200 h using standard conversions (Rosenberg et al. 1983). I weighed the fuel sticks to the nearest 0.1 g daily, between 1200 and 1400 h, until they dried below 12% moisture content.

Data were analyzed using non-linear regression, with vegetative cover as the independent variable and number of days for the fuel sticks to reach 12% moisture content as the response variable. Linear regression was used to relate total cover to mean minimum relative humidity and mean maximum temperature.

Test Fires

To further test the influence of treatment-induced changes in micro-environmental conditions on the forest's susceptibility to fire, I carried out a series of test fires in 4 m² square plots located just outside of the LTSRP plots. In the first experiment, I set 99 test fires during three consecutive days in early October 2001 (late dry season). Although 4 mm of rain fell 2 days before the trials, before that event no rain fell for 1 week. Test fire plots were located across the full range of cover conditions found in the treatment plots. All plots were within 25–300 m of the principal logging road and within 5–50 m of primary skid trails, to facilitate water transport and for safety.

Using methods adapted from U.S. Forest Service fire research in Brazil (personal communication, D. Sandberg and E. Alvarado, August 2001), I established 33 replicate sites for conducting experimental fires. A replicate consisted of a center point in which I placed a standard 10-h pine fuel stick and a litter sample in a nylon mesh bag for

measuring moisture content surrounded by three test fire plots each separated by 1–2 m. I also placed a Hobo data logger at 6 of the sites to record temperature and humidity over the range of cover conditions among all sites. Test fire replicates were at least 25 m apart and located to avoid steep slopes, dense Heliconia patches, and major vine tangles.

Before attempting to burn the plots, I estimated cover in 6 vertical strata using the grid method described above from the center of each of the 99 test fire plots. To control for variation in the presence of 100-h and 1,000-h fuels, I removed woody debris > 2.5 cm diameter from several test plots. This step also helped increase my confidence that the results were due to microclimatic factors and the quantity and moisture content of 1-h and 10-h fuels. To assess the quantity of 1-h fuels, I measured litter depth in ten locations (corners, perimeter midpoints, and two points near the plot center) to the nearest mm. I also collected a 20 cm × 20 cm litter sample from the center of each site using the method described above to assess 1-h fuel moisture content. Finally, the percentage of live vegetation below 1 m height (including ferns as well as herbaceous and woody vegetation) covering each sample plot was estimated.

To prevent fires from escaping beyond the plots, a 50 cm safety buffer was established around their perimeter 2–3 hours before starting the test fires. Specifically, all leaf litter and larger fuels were removed so that any fire reaching the plot edge would encounter mineral soil. Thus, all test fires eventually self-extinguished within the plot's borders.

I started the test fires at 1200–1430 h each day by igniting 50 ml of diesel that was dripped over a small area (400 cm²) in the center of each plot. As the fires were set, the fuel sticks and litterbags were weighed, the temperature and relative humidity were

measured with a digital max/min thermohygrometer (Thermo-Hygro, Control Company, Friendswood, Texas, USA), and wind speed (m/s) was estimated by measuring the distance a feather dropped from 2 m flew and the time it took to land. Vapor pressure deficit was calculated as described above. The amount of time flames were visible in each plot was recorded. After all the plots burned, I measured the maximum distance (0 to 90 cm) fire carried from the ignition zone in each plot and visually estimated the percent of each plot that burned. I repeated this experiment in June and July 2002 (in an area adjacent to Block 3 harvested 1–3 months previously) to quantify the extent to which intensifying management extends the fire-prone season.

After transforming percentage data (arcsine square root), the effects of total cover, litter depth, vapor pressure deficit, wind, and 10-h and 1-h fuel moisture content on the percent area of the plots that burned were evaluated with path analysis using SAS version 9.0 (SAS Institute, Inc., Cary, North Carolina) and procedures described by (Mitchell 2001). Path analysis allows hypothesized causal relationships (both direct and indirect) among independent and dependent variables to be tested via a series of multiple regressions (Schemske and Horvitz 1988, Mitchell 2001).

To quantify the persistence of any elevation in fire susceptibility due to intensification of management, I conducted an additional trial to compare the ability of fire to carry in forest logged at 3 different times. This trial, conducted in August 2002, was carried out near Block 2, near Block 3, and in an area logged in 1999. Block 3 had just been logged and hence was termed the 0-year treatment. Block 2 was logged 1 year previously (1-year) and the 1999 area was logged 3 years previously (3-year). Two research teams burned 10 plots per day at 1200–1430 h in each treatment. In contrast to

the criteria described above for selecting plot locations, I placed plots in the most severely disturbed sites (i.e., large felling gaps and primary skid trails) I could find in each of the three areas. After arcsine square-root transformation for percentage data, one-way ANOVA was used to compare the means of total cover, litter depth, 10-h fuel moisture, vapor pressure deficit, and plot area burned among the 3 treatment blocks. In the two cases with unequal variances among treatments, a Kruskal-Wallis test was used (test statistic, H). Post-hoc comparisons (Tukey or Mann-Whitney U) were conducted to specify which treatments differed.

Calculation of Fire-Prone Days

A simple model was used to calculate the number of days La Chonta is prone to fire in response to each management treatment in an average year and a dry year. The model is based on the assumption that the number of consecutive rainless days is a good predictor of fire susceptibility. It also depends on the relationship between canopy cover and the dry-down rate of 10-h fuels that was experimentally derived (see above).

The number of fire-prone days per month (F) was calculated as a function of f_o , fire-prone days for forest patches with very sparse vegetative cover (=open; total cover <110%); f_m , fire-prone days for patches with intermediate cover (=mid; total cover 110 to 210%); and f_c , fire-prone days for patches with dense cover (=closed; total cover >210%). Thus,

$$F = f_o * C_o + f_m * C_m + f_c * C_c$$

where C_o , C_m , and C_c represent the proportion of each treatment plot consisting of “open,” “mid,” and “closed” vegetative cover, respectively. Values for C were obtained from the assessment of treatment impacts on cover. The model weights the number of

fire-prone days for open, intermediate, and closed canopy conditions by the proportion of the forest in each condition.

Fire-prone days for each cover class were calculated with the following procedure. First, I examined the daily rainfall records for La Chonta, which were available for 1998 to 2002, and defined a rainfall event as being a one-day measurement of at least 5 mm of precipitation, which included 98% of the rainfall records. Second, I counted the number of consecutive rainless days required for 10-h fuels to dry sufficiently to ignite for open, intermediate, and closed forest patches. Based on the results of the cover and dry-down experiments (described above), I assumed that 10-h fuels become flammable after 3 consecutive rainless days in open forest patches, after 6 consecutive rainless days in intermediate forest patches, and after 9 consecutive rainless days in closed forest patches. For example, if in a particular month two rain events were separated by 10 consecutive rainless days, open patches would be fire-prone for 7 days, intermediate patches for 4 days and closed patches for 1 day. The monthly tallies of fire-prone days (based on consecutive rainless days) for open, intermediate and closed forest were used as values for f_o , f_m , and f_c , respectively. This equation was used to calculate F on a monthly basis for each treatment for the 5-year period 1998–2002. The results for each treatment were compared by visual inspection of box plots of these values and of summary statistics. Because the inter-annual, within treatment variation greatly exceeded variation among treatments, treatment effects were not compared with inferential statistics.

Results

Treatment Effects on Forest Structure

Between 35 and 44% more trees were harvested per ha from the intensive treatment plot than from the other two harvest treatment plots (Table 1-1). The corresponding basal

area and volume harvested from the intensive plot was also greater than the other treatments, but the difference between the normal logging and intensive treatments was smaller than expected due to the greater average diameter of harvest trees in the normal treatment than in the intensive treatment plot (Table 1-1). The intensive treatment killed 41% more trees (≥ 10 cm dbh) than the improved treatment and 33% more than the normal treatment (Table 1-1).

Treatment impacts on forest structure were relatively modest. Six months following treatment, the harvest treatment plots had only 10–25% more gaps and building-phase forest (vegetation ≤ 8 m) than the control plot. Similarly, the proportion of the plots with mature forest (vegetation > 16 m) was 20% less in the harvest treatments than in the control treatment, but only 30% of the control plot comprised mature forest. Average horizontal distances to gaps were shorter in the intensive management than in the improved harvesting and control treatments ($F_{3, 12} = 6.3, P < 0.01$), but were similar in the intensive management and normal harvest treatments. The area disturbed by felling and skid trails was similar among the harvest treatments (Table 1-2). The harvest treatment plots retained less cover than the control treatment plot in the 8–16 m stratum ($F_{3, 12} = 8.2, P < 0.01$), but cover in this stratum was similar among the harvest treatments. When all cover strata were combined (maximum cover = 600%), only the normal harvest and intensive management treatments retained less cover than the control ($F_{3, 12} = 7.7, P < 0.01$); total cover was similar in the intensive management and normal harvest treatments (Table 1-3). Only 6% of the intensive treatment plot comprised patches with sparse cover ($\leq 110\%$).

Treatment Effects on Fuel Loads

Based on 3,575 m (325 transects) inventoried for woody debris 6- and 15-months post-harvest, the treatment plots differed most notably in the quantity of coarse woody debris encountered. The intensive management plot contained twice the quantity of 1,000-h fuels as the normal and improved harvest plots and 25 times the quantity as the control plot. In addition, about 60% more 100-h fuels were encountered in the intensive management plot than in the control plot and about 30% more were tallied in the intensive management plot compared to the normal and improved harvest plots (Table 1-4). Similarly, the variation in spatial distribution of fuels increased with treatment intensity. Compared to the control treatment, the intensive management treatment increased the variation in the quantity of 1-h fuels by 58%, 100-h fuels by 101%, and 1,000-h sound fuels by 121% (Table 1-4).

Because the results of the 6-month and 15-month post-harvest woody debris assessments were similar ($F_{1, 317} = 1.3$; $P = 0.27$), the data from both were pooled. The assessments revealed that (i) greater fuel loads were present in the harvest treatments than in the control treatment (Table 1-5), and (ii) total mass of woody debris (all size and decay classes) was greatest in the intensive treatment (Table 1-5), but differences among harvest treatments were not significant. The greater mass of sound 1,000-h fuels in the harvest (especially the intensive) treatments compared to the control treatment accounted for most of the difference in mass of woody debris.

The harvest treatments reduced leaf litter depths ($H = 31.0$, $P < 0.01$, Figure 1-1a) relative to the control treatment six months after logging (during the early rainy season), but among harvest treatments, litter depth did not differ (Figure 1-1a). In contrast, litter depth did not differ among any of the treatments at the beginning of the subsequent dry

season (15 months post-harvest; Figures 1-1b) although the trend was similar. Only the intensive harvest treatment had lower litter mass 15 months post-harvest than the control.

Effect of Cover on Fuel Dry-Down Rates

Vegetative cover had the expected effects on both microclimate and fuel dry-down rates. Maximum understory temperatures were lower and minimum relative humidities remained higher with increasing vegetative cover during the dry season (Figure 1-2a). Despite faster dry-down rates of fuels in sites with sparse cover ($F_{1,46} = 16.10$; $P = 0.0002$), 10-h fuels dried down enough to ignite in all sites (Figure 1-2b). Specifically, during the mid-dry season, 10-h fuels dried down to 12% moisture content within 3 to 6 days after wetting in open sites (total cover < 110%) and within 7 to 10 days in shaded sites (total cover > 210%; Figure 1-2b).

During the early dry season of 2002, vegetative cover similarly slowed dry-down rates, but it was not possible to determine by how many days. A wetter than average May caused the moisture content of 10-h fuels under most cover conditions to remain well above 12% throughout the experiment. Ten-hour fuels dried down to 12% moisture content (2–3 days after soaking) only in the most open sites.

Fire Trials

Late dry season

During the early October 2001 fire trials, the area of each plot burned varied substantially with some plots burning entirely and others not at all. Of the 99 plots tested, only 21% burned completely (> 90% charred). However, fire carried to at least 1 plot edge in 57% of the plots. In cases where fires did not reach the plot edge, only 15% of the plot burned on average (range: 5–35%). Fires did not carry at all in 18% of the plots.

The plot area that burned differed among the three days of the 2001 trial (Table 1-6, $H = 9.2$, d.f. = 2, $P = 0.01$). Because neither cover nor litter depth varied over the three days, the variation in area burned among days was probably attributable to the cooler, more humid, less windy, and cloudier weather on the third day compared to the first two days of the trial (Table 1-6). Because the principal aim was to quantify the effects of key factors on area burned across sites, the three-day averages per site were used in the path analysis.

Path analysis confirmed the expected effects of total cover, litter depth, vapor pressure deficit, and 1-h fuel moisture content on percent area of test plots burned (Figure 1-3, Table 1-7). Despite the influence of these factors on area burned, a large proportion of unexplained variance remained (Figure 1-3), which was consistent with the observation that several plots in deep shade burned while some plots with sparse cover and apparently ample fuel did not. The moisture content of 10-h fuels in all sites tested was at or below the theoretical threshold for combustion (Table 1-6) and did not affect area burned (Figure 1-3, Table 1-7). Wind speeds throughout the trial were low (Table 1-6) and also did not directly affect area burned (Figure 1-3, Table 1-7).

Early dry season

During the 11–12 June 2002 fire trials, no test plots burned. Despite 12 rainless days, mean minimum relative humidity remained above 70% during the trials.

In July 2002, only 3 of the 30 plots tested burned completely, whereas less than 30% of the test area was charred in the remaining plots. Total cover was sparse (35 to 110%) in the three plots that burned, whereas in the plots that did not burn total cover ranged from 30 to 415% (mean: 254% \pm 21). Analysis of paths for which sufficient data existed indicated that 10-h fuel moisture increased with increasing total cover (partial

regression coefficient = 0.87, $P < 0.001$, $R^2 = 0.75$), and in turn area burned increased with decreasing 10-h fuel moisture (partial regression coefficient = -0.79, $P = 0.01$, $R^2 = 0.69$).

Total cover did not affect litter depth and litter depth did not influence area burned.

Persistence of treatment impacts on fire susceptibility

In the August 2002 fire trials to compare the fire susceptibility of forest areas logged 0, 1, and 3 years previously, only 10 of 94 plots burned. Nevertheless, in the recently logged area (0-year), 8 of 34 plots burned compared to only 1 of 31 plots in the area logged 1 year previously (1-year) and 1 of 30 plots in the area logged 3 years (3-year) previously.

When the data for the three days of the trial were averaged by time since logging, the mean area of the test plots burned was nearly three times greater in the 0-year treatment (27%) than in the 1-year (9%) and 3-year (10%) treatments indicating that plots in the recently logged area were more flammable than plots in the older logging treatments ($F_{4, 45} = 41.5$; $P < 0.0001$; Table 1-8).

Analysis of paths (by time since logging) for which sufficient data existed indicated greater total cover increased 10-h fuel moisture and litter depth only in the 1-year treatment. Litter depth, but not 10-h fuel moisture, in turn influenced area burned but only in the 3-yr treatment. Litter in the 0-year treatment was about twice as deep as in the 1- and 3-year treatments (Table 1-8) and about the same as the litter depth measured 3 months post-harvest during the late dry season of the 2001 fire trials (3.3 ± 0.9 cm; $n = 99$). Fuel moisture did not influence area burned in any of the treatments. Although fuels were drier in the 0-year treatment, 10-h fuel moisture was at or below the theoretical ignition threshold in all treatments (Table 1-8).

Fire-Prone Days

Analysis of 5 years of rainfall records revealed that long (~20 days) rainless periods are common in La Chonta. About 198 ± 52 mm of rain falls each month during the wet season, but only 60 ± 31 mm of rain falls monthly during the 6 mo dry season and only 36 ± 20 mm of rain falls in La Chonta during each of the driest months (June to August).

Long rainless periods in all months strongly influenced the results obtained from the model used to forecast fire-prone days. The number of fire-prone days ranged from 5 in February (the wettest month) to 26 in July and August for open sites (cover < 110%), from 1 in February to 24 in August for intermediate sites (cover 111–210%), and from 1 in February to 22 in August for closed sites (cover > 210%). When these data were used to forecast fire-prone days for each cover class, the number of fire-prone days in any given month was similar among treatments and depended much more on the strength of the dry season than on the treatments (Figure 1-4). For example, in an average year the number of fire-prone days in August ranged from 19.1 in the un-logged control plot to 19.5 in the intensive plot. In a drier than average year, all plots would be fire-prone for 31 days in August. These estimates of fire-prone days were based on the cover conditions in the treatment plots 6 months post-harvest after which the small differences among treatments further diminished.

Discussion

Treatment Effects on Forest Structure

Impacts of the silvicultural experiment in La Chonta on forest structure were modest and similar among treatments despite the greater number of trees and lianas killed in the intensive management treatment. This similarity in experimental treatment impacts

was attributable in part to the smaller average diameter of harvested trees in the intensive management plot compared to the normal and improved logging plots. In addition, although the intensive management treatment doubled the harvest intensity relative to what is typically applied in similar forests in Bolivia, it was mild when compared to other logging operations in the tropics where harvest volumes are 2–10 times greater than those observed in this study (Putz et al. 2001).

Although the intensive management treatment had more gaps than the normal or improved logging treatments, the average distance to gaps differed by only a few meters among the treatments. Considering that edge effects on understory microclimate can penetrate at least 40–60 m (Kapos 1989, Didham and Lawton 1999, Cochrane and Laurance 2002) and the fact that half the canopy trees in La Chonta lose their leaves during the height of the dry season, differences among treatments are probably insufficient to markedly affect fuel dry down rates. Among harvest treatments, vegetative cover differed only in the mid-canopy strata, but the modest differences in total cover need to be considered in reference to the relatively open canopy characteristic of this semi-deciduous forest even before logging. In fact, the most striking result was the high background level of disturbance in La Chonta: 30% of the control plot comprised natural gaps or young forest.

Due to its open canopy, La Chonta is already very susceptible to fire even in the absence of logging. Although elevated fuel loads and decreased canopy cover resulting from mahogany extraction probably exacerbated the severe fires of 1995 (Pinard et al. 1999b, Mostacedo et al. 2001, Gould et al. 2002), large swaths of apparently undisturbed forest also burned. Similar fires have occurred in undisturbed forests of the eastern

Amazon, but only after several years of drought (Uhl and Kauffman 1990, Nepstad et al. 1995, Nepstad et al. 1999b). In contrast to these forests, La Chonta receives 300 to 500 mm less rainfall annually and is semi-deciduous, factors that help explain its fire susceptibility even without logging.

Treatment Impacts on Fuel Loads

The average fuel load (including woody debris and leaf litter) recorded in the un-logged control area in La Chonta (~27.5 Mg/ha) is on the low end of values reported for primary forests in the Amazon. For example, fuel loads twice as great were reported from the eastern Amazon (Uhl and Kauffman 1990) and Venezuela (Kauffman et al. 1988, Delaney et al. 1998). The mass of 100-h fuels in La Chonta was 10 times lower (1.6 vs. 16.8 Mg/ha) than what Cochrane et al. (1999) measured in un-logged forests in the eastern Amazon. The relatively low mass of dead and down fuels in La Chonta is probably attributable to the low tree biomass, which is an expected consequence of lower rainfall (Murphy and Lugo 1986) and high liana density (Alvira et al. 2004). Similarly low fuel loads were found in second growth forests in Brazil (Uhl and Kauffman 1990).

Relative to the control, fuel loads were doubled by the normal logging treatment and tripled by the intensive treatment. These increases were mainly attributable to a greater amount of sound 1,000-h fuels resulting from harvest damage and residues that persist for at least 15 months post-treatment. The relative increase in fuel loads from intensive management compared to the un-logged control was similar to that reported by Uhl and Kauffman (1990). In their study, however, the magnitude of woody debris inputs (150 m³/ha) was much greater than reported here. This difference might be attributable to the size of trees harvested, harvest practices, and to the greater overall

volume (50 m^3 vs. 18 m^3) and number of harvested trees (8 vs. 5 ha^{-1}) in their study site in Brazil.

Although the harvest treatments increased woody fuel loads, they decreased leaf litter depth (6 months post-treatment) and mass (15 months post-treatment) compared to the control, with the lowest values in the intensive treatment plot. These results differ from those reported by Uhl and Kauffman (1990); in their study site, the mass of fine fuels was 30% greater in the logged vs. the control area. Site factors (e.g., greater leaf area index and litter production in the eastern Amazon) probably explain most of this difference, but the timing of the censuses might also be relevant. Uhl and Kauffman (1990) estimated litter mass a few months post-logging, whereas in this study litter mass was quantified 15 months post-logging, which corresponded to the early dry season when leaf litter is typically sparse (personal observation).

In this study, it appears that the harvest impacts on fuel loads are more likely to affect potential fire severity than fire susceptibility. The quantity, arrangement, and moisture content of fine fuels, including litter, determine to a large extent the susceptibility of a particular area of forest to fire (Stott 2000, Cochrane 2003). Once a fire ignites, the arrangement, quantity, and moisture content of larger fuels influence whether combustion is sustained and also determine the fire's severity (Stott 2000). Although this study did not assess fire behavior, it is nevertheless reasonable to infer that fire severity would be greatest in the treatments with the greatest quantity of fuels, especially 1,000-h and larger fuels. The harvest treatments at La Chonta would increase fire severity relative to the control, but the potential for severe fires would be greatest in the intensive treatment because of the three-fold increase in 1,000-h fuels relative to the

normal treatment. The greater quantity of 1,000-h fuels in the intensive treatment plot implies that if a fire were to occur, it would smolder longer and be harder to extinguish (Cochrane 2003), and consequently cause higher tree mortality rates (Kauffman 1991) than in the other treatment plots.

Vegetative Cover and Fuel Dry-Down Rates

As described for forested areas throughout the tropics (Walsh 1996), understory vapor pressure deficits decreased with greater total cover in La Chonta. That the effect of cover on vapor pressure deficit was strongest early in the dry season and weakest in the mid-dry season indicates that once the forest dries, not even sites with dense cover retain much moisture. Only about half of the canopy species and canopy trees retain their leaves during the greatest period of water stress (i.e., July–August; Justiniano, unpublished data).

The semi-deciduous canopy of La Chonta differs from the evergreen forests of the eastern Amazon, the canopies of which remain closed (thanks to deep rooting of most tree species) despite equally long and severe droughts (Nepstad et al. 1995). Retention of an evergreen canopy in the eastern Amazon is considered to be the key attribute that provides fire immunity during normal years because it prevents desiccation of the understory vegetation and surface fuels (Nepstad et al. 1995).

Ten-hour fuels in the most open sites dried below the moisture content threshold within 3–6 days, a result similar to what Holdsworth and Uhl (1997) found in the eastern Amazon. In contrast, 10-h fuels required only 7–10 rainless days to dry enough to ignite even in the most shaded sites in La Chonta, whereas 10-h fuels remained above threshold levels at which ignition could occur throughout the dry season in un-logged forests of the eastern Amazon (Uhl and Kauffman 1990, Holdsworth and Uhl 1997) and Venezuela

(Uhl et al. 1988). These results suggest that the understory microclimate in semi-deciduous forests like La Chonta apparently is much drier than the evergreen forests elsewhere in the Amazon where similar fire studies have been conducted, and that open sites in La Chonta can burn after only 3 rainless days, while most undisturbed sites can burn after only 10 rainless days.

Fire Trials

The extent to which experimental fires carried depended on vegetative cover, litter depth, relative humidity, and fuel moisture content. These factors are well known to influence forest flammability (Stott 2000), but they only explained 59% of the observed variation. In the late dry season (October 2001) and only a few months after logging, many plots in sites with sparse vegetation and apparently sufficient litter did not burn completely, and conversely, some plots in densely shaded areas burned completely or nearly so. This latter observation contrasts with results from undisturbed evergreen forests in Amazonian Brazil (Uhl and Kauffman 1990, but see Holdsworth and Uhl 1997), Venezuela (Uhl et al. 1988, Kauffman and Uhl 1990), and Indonesia (Siegert et al. 2001, van Nieuwstadt et al. 2001), which remain fire resistant in the absence of severe disturbances or El Niño associated droughts. The deciduous nature and open canopy structure of La Chonta apparently renders it fire-prone even in the absence of logging or severe drought.

In the early dry season, at least at the management intensities tested in this study, La Chonta is not very fire-prone. The failure of any plots to burn in June 2002 supports this conclusion. Moreover, few if any ignition sources exist during the early dry season because most small farmers and ranchers wait until July or August to set fires, and lightning initiated fires are rare (Tutin et al. 1996, Stott 2000, Saarnak 2001). All of the

destructive fires of the past 4–5 years (since a fire monitoring system was established) occurred in August or September (Política y plan nacional de prevención y control de incendios forestales en Bolivia. 2002. Ministerio de desarrollo sostenible y planificación, La Paz, República de Bolivia). Finally, fine fuels are much less available in the early dry season than they are toward the end of the dry season after half the canopy trees shed their leaves.

Factors influencing fire susceptibility

The key factors explaining variation in area burned varied somewhat during the dry season, but moisture content of fuels, litter depth, and vapor pressure deficit were always important. The lower number of plots that burned on day 3 of the October 2001 fire trial when conditions were overcast and humid exemplified the influence of low vapor pressure deficit, which resulted in higher moisture contents of the short time-lag fuels. Low vapor pressure deficit during the July 2002 trial similarly appeared to render most plots non-flammable.

Fuel moisture content, a critical determinant of forest flammability (Stott 2000), influenced the area of plots burned to a different extent during the dry season. Specifically, moisture content of 10-hour fuels was a better predictor of the area of plots burned earlier in the dry season because the moisture content of 10-h fuels was about the same regardless of cover in the late dry season. Cochrane's (2003) suggestion that 1-h fuel moisture would be a more appropriate predictor of fire susceptibility than 10-h fuel moisture was supported by the path analysis of the late dry season fire data. Nevertheless, the use of 10-h fuel dry down rates in the fire-prone days model is considered valid because 10-h fuel moisture did explain whether plots burned in the early-dry season. The packed arrangement of 1-h fuels on the forest surface explains

why they may remain moister than 10-h fuels (Uhl et al. 1988), which were suspended 25 cm above the surface.

Differences in litter depth among plots also helped explain whether plots burned. Fuel coverage and quantity are key determinants of whether fires will carry across the forest floor (Stott 2000). Regardless of time during the dry season, few plots burned if they had litter less than 2.1 cm deep. It is conceivable but unlikely that sufficient litter would accumulate by the end of the dry season in the areas logged 1 and 3 years previously to render them more flammable because the senesced leaves of the pioneer species occupying the disturbed areas tested were already on the ground.

As reported for other tropical forests (Cochrane 2003), the extent to which plots burned decreased with increasing cover in La Chonta, but this effect was strongest in the early dry season. Apparently, only sites in or very near large gaps are likely to be fire-prone early in the dry season. To the extent that intensive management creates more gaps, it will elevate fire susceptibility in the early dry season. This differential effect should be smaller, however, in the late dry season because by then fuels are dry enough to ignite regardless of cover. In summary, intensified management, at least to the extent tested in La Chonta, did not appreciably elevate fire susceptibility compared to the un-logged control or normal management practices, at least in the late dry season.

Persistence of treatment impacts on fire susceptibility

The modest increase in susceptibility to fire in the early dry season resulting from intensive timber stand management in La Chonta seems to persist only for the year immediately following treatment; almost none of the plots in severely disturbed sites that were logged 1 and 3 years previously burned. In contrast, about one-fifth of the plots burned in an area logged 2–4 months previously suggesting that the elevated fire

susceptibility associated with intensifying management in the early- to mid-dry season would become indistinguishable from normal harvest practices within 1 year. In the eastern Amazon, Holdsworth and Uhl (1997) found that re-growth in 3-year old logging gaps slowed fuel dry down rates rendering such gaps fire resistant. In La Chonta, 10-h fuels were drier in the area logged immediately prior to the fire trials than in the older logging areas, but even fuels in areas logged 1 and 3 years previously were dry enough to burn. Rather than fuel moisture, depth of fine fuels was the more important factor in the few plots that burned in the areas logged 1 and 3 years previously.

Treatment impacts on number of fire-prone days

The most striking result from the model employed to estimate the number of days the forest is fire-prone in response to each treatment was that the effects of inter-annual variability in rainless periods greatly exceed any differences among treatments. For example, only 22 mm of rain fell in 2 rain events from July to September 1999, which resulted in 76 fire-prone days for closed forest patches according to the model. During the same period in 2000, 215 mm of rain fell in 7 rain events, which resulted in only 47 fire-prone days. In an average year, the long rainless periods in the middle of the dry season resulted in very minor differences (maximum of 4 days) in fire-prone days between open, intermediate and closed sites. Considering the modest treatment impacts on cover, the difference in fire-prone days among treatments regardless of month was negligible.

Among the many assumptions inherent in the model I used to predict the number of fire-prone days, the most important are that 12% moisture content is a valid threshold on which to base fire susceptibility and that the number of consecutive rainless days is the best predictor of fire susceptibility. A more elaborate model might include fuel loads

(especially litter depth and arrangement) as well as vapor pressure deficit, both of which helped explain the test fire results.

Conclusions and Management Implications

Four major conclusions can be drawn from the previous discussion. First, un-logged seasonally deciduous forests like La Chonta appear to be very susceptible to fire throughout much of the dry season. This finding contrasts with results reported for intact evergreen forests of the eastern Amazon, which remain fire resistant except during the driest years. Second, the range of timber harvest intensities assessed in this study had a trivial impact on the forest's susceptibility to fire, and this small impact diminished rapidly with time. Therefore, there appear to be only very modest and short-lived tradeoffs between doubling the management intensity in an effort to secure adequate regeneration and growth for sustained timber yields and fire susceptibility in these forests. Assuming the forest can be adequately protected from ignition, especially during the year after harvesting, silvicultural activities at the intensities carried out in this study should not be viewed as creating excessively threatening conditions for fire. These conclusions must be considered, however, in the context of the substantial increase in coarse woody debris resulting from intensive management. Should a fire occur, it would be most severe where the forest is managed intensively because of the increased quantity of 1,000-h fuels.

Based on these conclusions, it is clear that better control of ignition sources to prevent fires must complement silviculture treatments to achieve sustained yields if these forests are to satisfy both production and conservation goals. To some extent, training forest crews in fire prevention and control techniques will help reduce fire damages to production forests. Vigilance against fires escaping from nearby pastures (or starting

within logging areas) should be concentrated in the same year as harvest activities, which is relatively easy if roads are designed as fire breaks. Moreover, forest managers should consider spatial arrangements of harvest units such that sufficiently wide buffers (Holdsworth and Uhl [1997] suggested 1 km) surround each unit at least for 1–3 years following harvest.

Unfortunately, controlling ignition sources in the Amazon will require a monumental shift in attitudes and practices and an equally large improvement in governance so that the positive economic and biophysical feedbacks that are making the Amazon Basin more fire-prone can be broken (Nepstad et al. 2001). A better understanding of fire science across the range of forest types in the Amazon will provide a sound basis for breaking these feedbacks (Cochrane 2003). Equally important is greater emphasis on multidisciplinary research that elucidates cultural and social uses and attitudes pertaining to fire (Roman-Cuesta et al. 2003), as well as an increase in interagency and intergovernmental cooperation. Considering the rapidly changing land use and climate in the region, unless greater priority is given to better defining and resolving the multiple dimensions of the fire problem in different biophysical and socioeconomic contexts, the kind of fire-prone forests found in La Chonta may become more common throughout the entire Amazon Basin.

Table 1-1. Impacts of timber harvesting and silvicultural treatments in Block 2 of the Long-term Silvicultural Research Project in La Chonta.

Parameter	Normal	Improved	Intensive
Plot area (ha)	25.9	27.8	25.0
Trees harvested per ha	3.3	2.8	5.0
Basal area (m ²) harvested per ha	2.1	1.4	2.7
Volume (m ³) harvested per ha	16.8	11.9	18.5
Mean (\pm se) dbh of harvested trees	84.3 \pm 3.5	77.7 \pm 2.8	70.7 \pm 2.1
Reduction in tree density (%) ^a	7.8 (11.8)	7.3 (11.1)	12.5 (17.9)

Source: unpublished data from the Bolivian Institute for Forestry Research (IBIF).

^aTotal percentage of trees harvested and killed (>10 cm dbh; based on differences in census 1 and 2). The number in parentheses refers to the proportion of trees > 40 cm dbh that was harvested.

Table 1-2. Percentage of each treatment plot in Block 2 of La Chonta observed in corresponding habitat classes based on point sampling along four 400–450 m transects in each treatment plot 6 months post-harvest.

Habitat Class	Control	Normal	Improved	Intensive
Undisturbed	62.3	35.8	39.2	28.4
Skid trail	0	5.9	5.2	4.9
Skid trail edge	0	12.4	10.5	9.8
Felling gap	0	16.0	9.9	15.0
Felling gap edge	0	15.1	14.9	22.6
Total harvest disturbed	0	49.4	40.6	52.3
Natural gap	7.7	4.1	3.0	5.5
Natural gap edge	30.0	10.7	17.1	13.8
Total natural disturbed	37.7	14.8	20.1	19.3
Total	100.0	100.0	100.0	100.0

Table 1-3. Summary of assessment of treatment impacts on forest structure showing means \pm standard errors for estimates of vegetative cover (%) in 6 vertical strata, total cover, maximum height, and horizontal distance to nearest gap.

Treatment	N	Vegetative cover (%)					Total	Maximum height (m)	Distance to gap (m)	
		0–1 m	1–2 m	2–4 m	4–8 m	8–16 m				>16 m
Control	377	52.9 \pm 1.1	29.4 \pm 1.2	41.7 \pm 1.6	67.0 \pm 1.3	64.4 \pm 1.6 ^a	29.0 \pm 1.6	284.4 \pm 3.3 ^a	13.8 \pm 0.4	10.3 \pm 0.4 ^a
Normal	338	47.6 \pm 1.4	27.2 \pm 1.3	35.4 \pm 1.6	55.7 \pm 1.5	54.8 \pm 1.5 ^b	21.7 \pm 1.5	242.4 \pm 3.9 ^b	12.4 \pm 0.4	7.4 \pm 0.3 ^{bc}
Improved	363	52.4 \pm 1.2	28.8 \pm 1.4	39.9 \pm 1.8	57.9 \pm 1.6	58.8 \pm 1.6 ^b	23.5 \pm 1.4	260.9 \pm 4.0 ^b	12.2 \pm 0.4	8.4 \pm 0.3 ^{ab}
Intensive	327	50.5 \pm 1.4	32.7 \pm 1.4	35.0 \pm 1.6	54.3 \pm 1.6	46.2 \pm 1.6 ^b	18.8 \pm 1.4	237.5 \pm 4.2 ^b	11.5 \pm 0.3	6.3 \pm 0.3 ^c

Notes: The maximum value for total cover = 600%. Estimates of all variables were made every 5 m (N = number of sample points) along each of four 450 m-long transects in each treatment plot. Different letters indicate differences among treatments at $P < 0.05$ based on 1-way ANOVAs in which sample means for each transect in each treatment plot were compared (n=4 per plot).

Homogenous subsets determined with a Tukey's post-hoc test.

Table 1-4. Mean quantity of woody debris encountered per meter of transect in La Chonta.

Treatment	N	Fuel size / decay class					
		1-h	10-h	100-h	1,000-h sound	1,000-h intermediate	1,000-h rotten
Control	79	17.00 (10.20)	5.00 (3.41)	0.27 (0.32)	0.00 (0.02)	0.02 (0.05)	0.04 (0.08)
Normal	77	20.21 (12.39)	4.74 (4.40)	0.48 (0.50)	0.06 (0.13)	0.05 (0.09)	0.04 (0.07)
Improved	82	24.27 (16.72)	4.40 (2.61)	0.45 (0.40)	0.05 (0.15)	0.03 (0.06)	0.03 (0.05)
Intensive	87	20.02 (16.09)	4.10 (3.11)	0.62 (0.65)	0.10 (0.26)	0.05 (0.10)	0.02 (0.04)

Notes: Values are the mean number of fragments of dead and down woody material measured in two censuses (6 months and 15 months post-treatment). Numbers in parentheses are standard deviations. Fuel sizes classified by diameter according to the fuel time-lag concept (see text): 1-h (<0.6 cm); 10-h (0.6–2.5 cm); 100-h (2.5–7.5 cm); and 1,000-h (> 7.5 cm). Fuel decay classes follow Delaney et al. (1998). N = total number of transects from the two censuses. Transect lengths varied by size class as follows: 1-h: 1 m; 10-h: 2 m; 100-h: 5 m; and 1,000-h: 11 m.

Table 1-5. Mean densities and mass estimates for each size and decay class of woody debris in La Chonta.

Fuel size/decay class	Wood density (g/cm ³)	N	Mass (Mg/ha)			
			Control ^a	Normal ^b	Improved ^b	Intensive ^b
1-hour	0.34 ± 0.01	174	1.4 ± 0.1	1.7 ± 0.1	1.9 ± 0.1	1.7 ± 0.2
10-hour	0.35 ± 0.03	146	4.3 ± 0.3	4.1 ± 0.4	3.8 ± 0.2	3.4 ± 0.3
100-hour	0.30 ± 0.01	144	1.6 ± 0.2	2.9 ± 0.3	2.8 ± 0.3	3.8 ± 0.4
1,000-hour sound	0.66 ± 0.06	86	0.3 ± 0.2	11.9 ± 4.0	11.2 ± 3.4	35.8 ± 12.5
1,000-hour intermediate	0.59 ± 0.06	72	7.3 ± 4.7	12.4 ± 6.3	11.4 ± 5.5	14.8 ± 5.3
1,000-hour rotten	0.47 ± 0.09	63	7.1 ± 1.9	8.3 ± 2.4	6.1 ± 1.4	3.7 ± 1.1
Total			22.0 ± 5.0	41.3 ± 8.0	37.1 ± 6.4	63.1 ± 13.9

Notes: Means (± standard error) based on averages from two censuses 6 and 15 months post-treatment. Fuel sizes classified by diameter according to the fuel time lag concept (see text): 1-h (<0.6 cm); 10-h (0.6–2.5 cm); 100-h (2.5–7.5 cm); and 1,000-h (>7.5 cm). Decay classes follow Delaney et al. (1998). Different letters next to treatments indicate significant differences based on 1-way ANOVA with masses log₁₀ transformed ($F_{3,321} = 3.81$; $P = 0.01$; $N = 79$ for control, 77 for normal harvest, 82 for improved harvest, and 87 for intensive management). Values shown are based on actual data, not the back-transformed data.

Table 1-6. Summary of 7–9 October 2001 (late dry season) test fires in La Chonta showing means \pm standard error for measured variables for each of the three consecutive days of the trial and the three-day averages.

	Max. burn (cm)	Area burn (%)	Relative humidity (%)	Temp. (°C)	VPD (kPa)	Wind speed (m/s)	Litter moisture (%)	10-h fuel moisture (%)	Total cover (%)	Litter depth (mm)
N	33	33	5	6	5	33	33	33	33	33
Day 1	74.5 \pm 5.7	45.0 \pm 5.7	40.4 \pm 4.6	35.1 \pm 0.9	3.5 \pm 0.5	0.6 \pm 0.0	17.5 \pm 1.5	10.2 \pm 0.2	199.8 \pm 10.8	32.1 \pm 1.5
Day 2	87.0 \pm 3.9	55.6 \pm 5.4	38.2 \pm 2.5	35.5 \pm 0.8	3.7 \pm 0.5	0.6 \pm 0.0	14.9 \pm 1.1	10.1 \pm 0.2	200.3 \pm 12.6	33.6 \pm 1.6
Day 3	67.1 \pm 3.2	34.1 \pm 5.2	50.4 \pm 1.6	30.3 \pm 0.7	2.3 \pm 0.4	0.4 \pm 0.0	18.5 \pm 1.4	12.0 \pm 0.2	206.3 \pm 12.4	34.1 \pm 1.8
Average	76.2 \pm 4.2	44.9 \pm 4.3	43.0 \pm 2.9	33.6 \pm 0.6	3.1 \pm 0.5	0.5 \pm 0.0	16.9 \pm 1.1	10.8 \pm 0.2	202.2 \pm 6.8	33.1 \pm 0.9

Notes: Test fires were set at 1200–1430 h in 33 sites per day representing the range of cover conditions found throughout the 4 management treatments 2–3 months post-harvest. Max. burn = maximum linear distance from the center toward the edge of the 2 m \times 2 m plot that burned; Area burn = percent surface area of each plot that burned; VPD = vapor pressure deficit; Total cover = sum of percent vegetative cover estimates for six vertical strata (maximum = 600%). Data for relative humidity and temperature are daily mean minimum relative humidity and mean maximum air temperature among 6 data loggers (at a height of ~25 cm) at sites across the cover range. The humidity sensor malfunctioned in one of the data loggers, hence N = 5. Vapor pressure deficits calculated from temperatures and relative humidities.

Table 1-7. Path coefficients, *P*-values, and proportion of variance explained by factors influencing area burned in October 2001 test fires in La Chonta determined by path analysis.

Dependent variable	Independent variable	Path coefficient	<i>P</i>	R ²
Litter depth	Total cover	0.51	0.001	0.24
	Unexplained	0.87		
Vapor pressure deficit (VPD)	Wind	0.51	0.001	0.45
	Total cover	-0.47	0.002	
	Unexplained	0.74		
10-hr fuel moisture	Total cover	0.38	0.023	0.39
	VPD	-0.35	0.034	
	Unexplained	0.78		
1-hr fuel moisture	Total cover	0.30	0.070	0.39
	VPD	-0.43	0.011	
	Unexplained	0.78		
Burn area (%)	VPD	0.40	0.043	0.59
	Wind	-0.26	0.092	
	Litter depth	0.66	0.000	
	10-hr fuel moisture	-0.19	0.279	
	1-hr fuel moisture	-0.43	0.014	
	Unexplained	0.64		

Notes: The sample size for this fire trial was 33 test fires. See Figure 1-3 for the path analysis.

Table 1-8. Summary of August 2002 fire trial in La Chonta showing means, standard errors, and ANOVA or Kruskal-Wallis results for total cover, vapor pressure deficit (VPD), average litter depth, 10-h fuel moisture content, and area burned of 4 m² plots by year post-logging.

Measure	0-yr	1-yr	3-yr	F	d.f.	<i>P</i>	<i>H</i>
Total cover (%)	119.9 ± 16.4 ^a	192.5 ± 12.0 ^b	204.3 ± 8.7 ^b	12.9	2, 47	0.001	
VPD (kPa) ²	5.4 ± 0.2 ^a	3.2 ± 0.1 ^b	3.2 ± 0.1 ^b	88.1	2, 6	<0.001	
Area burned (%)	26.7 ± 5.5 ^a	8.7 ± 3.3 ^b	9.8 ± 2.6 ^b	7.2	2, 48	0.002	
Litter depth (mm)	3.5 ± 0.3 ^a	1.4 ± 0.1 ^b	1.5 ± 0.1 ^b			<0.001	29.6
10-h fuel moisture (%)	9.0 ± 0.4 ^a	12.2 ± 0.5 ^b	12.5 ± 0.4 ^b			<0.001	23.1

Notes: N=17 plots per treatment, except in the 0-yr treatment where N=15 for 10-h fuel moisture, and N=16 for total cover. Percentages were arcsine square root transformed. Means for VPD are based on 3 data loggers per treatment for the 3 days of the trial. Different letters indicate differences between treatments based on post-hoc comparisons with Tukey or Mann-Whitney U tests.

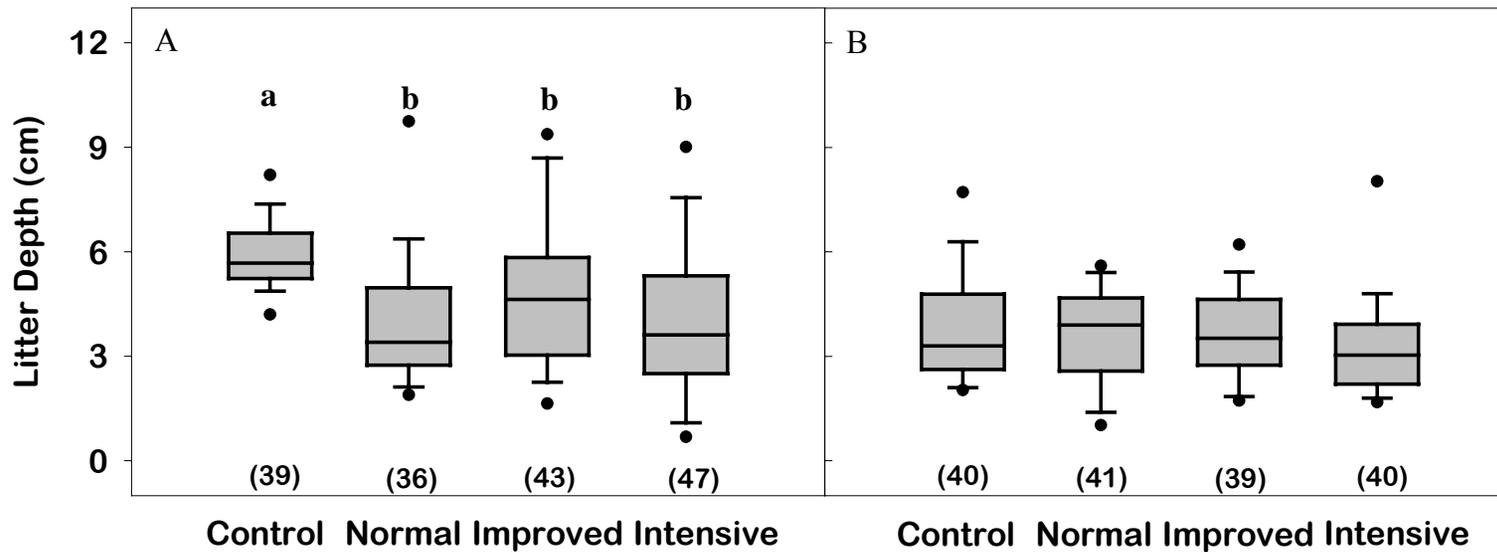


Figure 1-1. Treatment impacts on litter depth during the rainy and dry seasons in La Chonta. A) Rainy season, 6 months post-harvest. B) Dry season, 15 months post-harvest. Boxes represent quartiles, whiskers the 10th and 90th percentiles, and dots the 5th and 95th percentiles. The solid line shows the median. Different letters indicate significant differences. Sample sizes are shown in parentheses.

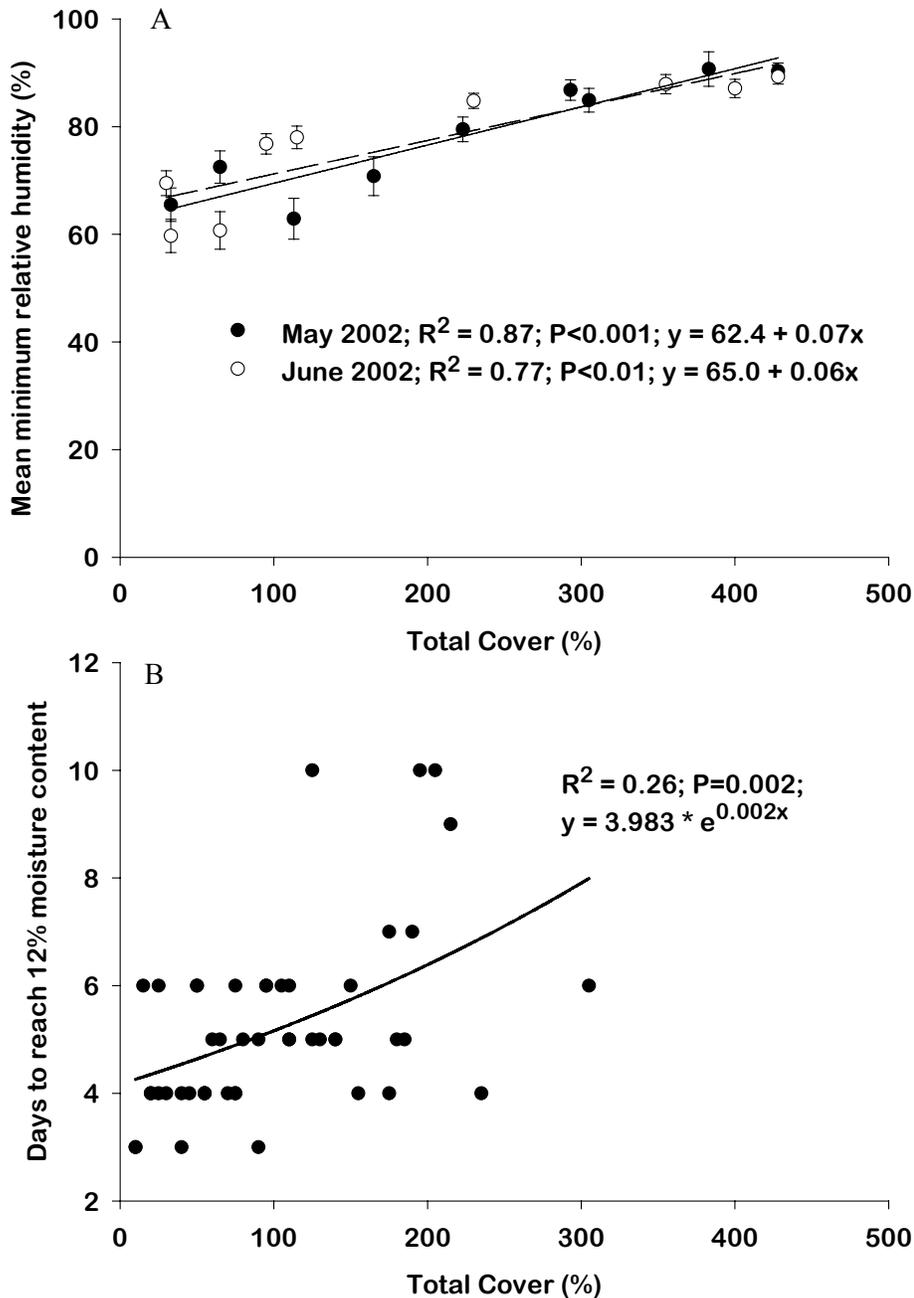


Figure 1-2. Effect of vegetative cover on understory microclimate and fuel dry-down rates in La Chonta during the early dry season of 2002. A) Mean minimum relative humidity. B) Number of rainless days required for 10-h fuels to dry down from saturation to 12% moisture. Total cover is the sum of percent cover estimates for six vertical strata. Points in A represent the means of midday relative humidity (%) measured with Hobo data loggers placed under different cover conditions 1–4 months post-harvest in Block 3. Error bars represent standard errors. Points in B represent the number of days each 10-h fuel stick required to reach 12% moisture content in July 2001. The R^2 and P -values are based on regression analysis.

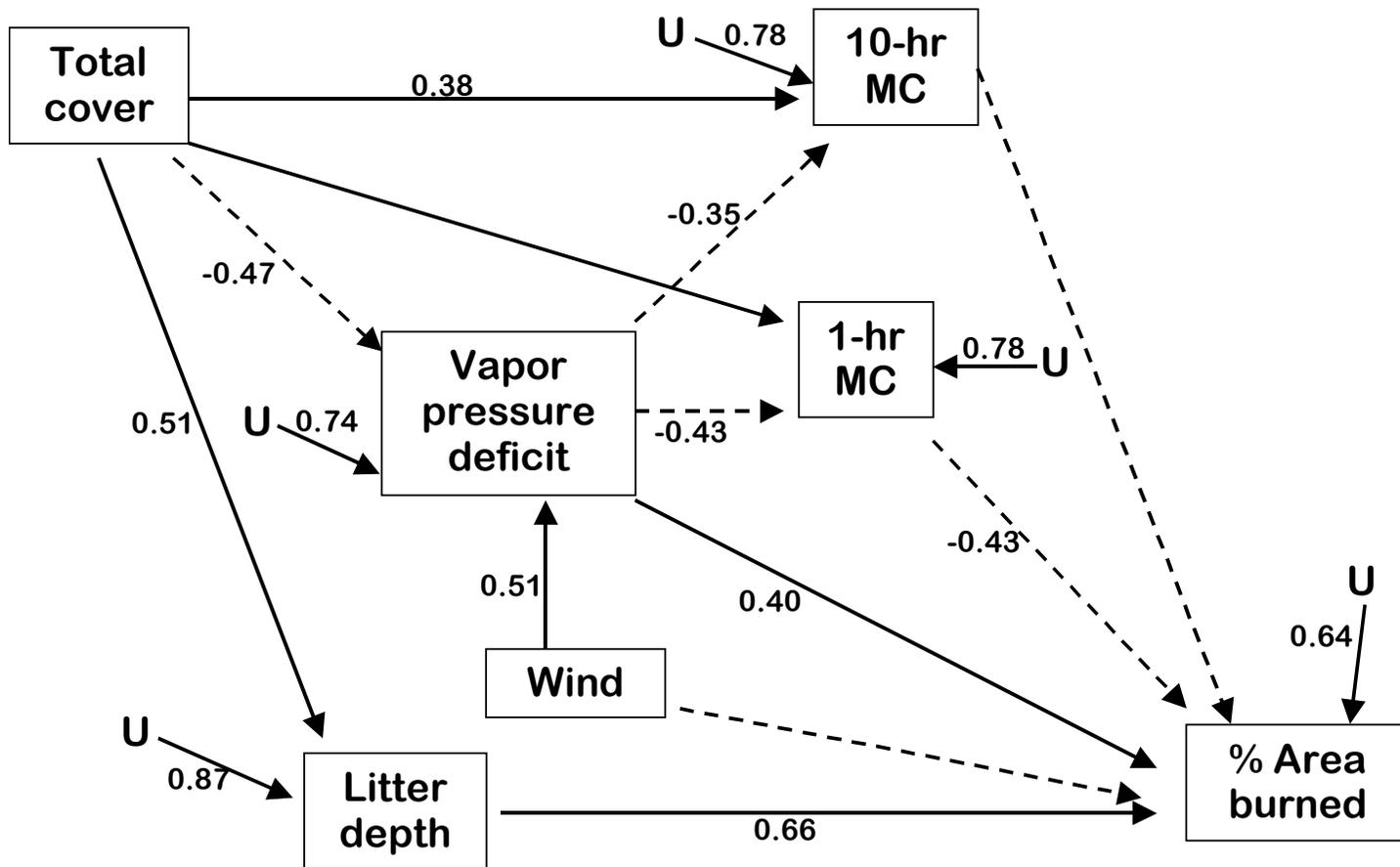


Figure 1-3. Path diagram for the effects of total cover, vapor pressure deficit, litter depth, wind, 10-h fuel moisture content (10-h MC), and 1-h fuel moisture content (1-h MC) on area burned (%) in the 7–9 October 2001 test fires in La Chonta. Arrows illustrate hypothesized paths of causation; solid arrows indicate positive effects and broken arrows negative effects. Arrows with adjacent values indicate significant effects at $P < 0.05$. Magnitude of the values indicates strength of the effects illustrated. Unmeasured factors affecting the variables are represented by “U”. See Table 1-7 for P - and R^2 -values.

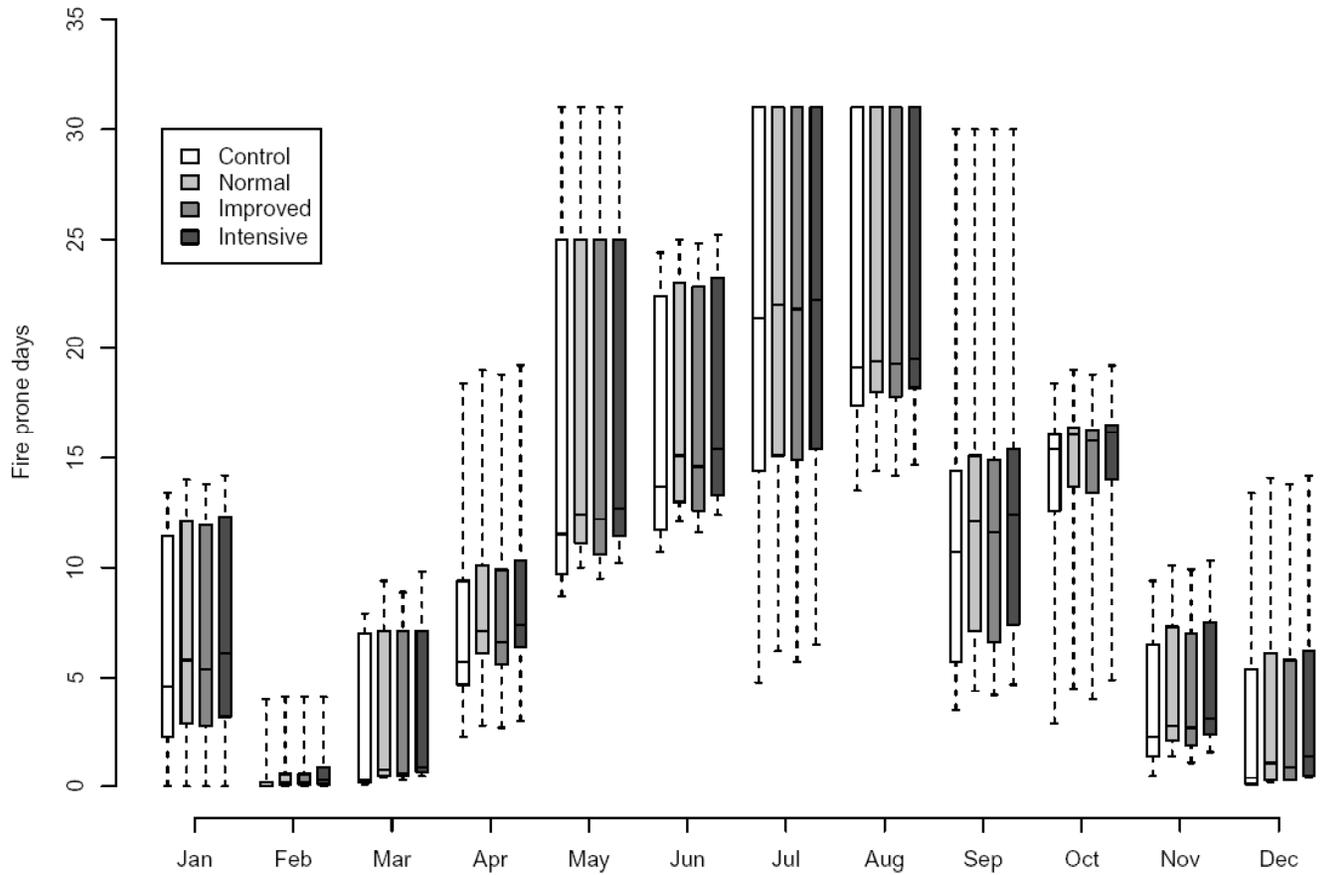


Figure 1-4. The number of fire-prone days per month predicted for each management treatment applied in La Chonta based on a model of consecutive rainless days and the proportion of each treatment plot consisting of “open” (<110% cover), “intermediate” (110–210% cover), and “closed” (>210% cover) forest patches (see text for details). Boxes represent quartiles, whiskers the 10th and 90th percentiles, and dots the 5th and 95th percentiles. The solid line shows the median.

CHAPTER 2
PROJECTING FOREST RESPONSES TO DIFFERENT SILVICULTURAL
TREATMENTS IN A SEMI-DECIDUOUS FOREST IN LOWLAND BOLIVIA

Introduction

Although tropical forests are valued for their rich biodiversity (Frumhoff and Losos 1998, Fearnside 1999a) and the myriad goods and services they provide (Johnson and Cabarle 1993), financial analyses based on available markets typically find that the timber production value of tropical forests is paramount (Pearce et al. 1999). Moreover, considering that most tropical governments view their forests as engines for sustainable development and given that protected areas alone are insufficient to conserve all of the tropics' biodiversity, the sustainable management of production forests has been promoted as a means to achieve both development and conservation goals (Dickenson et al. 1996, Chazdon 1998, Poore et al. 1999, Whitmore 1999). Unfortunately, managing tropical forests sustainably, or even just for sustained timber yields (STY), remains an elusive challenge for many reasons not the least of which is the limited information about the silvicultural requirements of commercial species used to set policies and management guidelines (Mostacedo and Fredericksen 1999).

Forest management in Bolivia has advanced substantially in the past decade (Nittler and Nash 1999) and an increasing number of forestry enterprises are seeking Forest Stewardship Council (FSC) certification (Blate et al. 2001, Fredericksen et al. 2003). Despite impressive advances, the Bolivian forest sector must contend with poor infrastructure, high transport costs, and limited market access, all of which constrain investments in training, field supervision, and silviculture.

In semi-deciduous forests, which account for 45% of Bolivia's timber production, foresters face a host of management problems that if left unresolved may undermine the aspirations of the forest sector and conservationists alike. First, application of reduced-impact logging practices alone is not a viable strategy for sustaining timber yields of the principally light-demanding commercial species because they regenerate poorly without intensive silvicultural treatments (Mostacedo and Fredericksen 1999, Fredericksen and Putz 2003). Second, these forests harbor lianas at densities that are among the highest recorded in the tropics (Perez-Salicrup et al. 2001, Alvira et al. 2004), which further inhibits commercial species regeneration and growth (Whigham 1984, Clark and Clark 1990, Putz 1991, Schnitzer et al. 2000, Gerwing 2001, Alvira et al. 2004, Grauel and Putz 2004). Third, most of these forests are highly susceptible to fire during the long and severe dry season, and because fires frequently escape from the agricultural matrix in which most remaining forests are embedded (Chapter 1). Finally, the current silvicultural rules were developed as first approximations because of limited knowledge of the population biology and silvicultural requirements of the species being managed (Fredericksen et al. 2003). Thus, questions remain about how to achieve STY.

In 2001, a silvicultural experiment was implemented to determine if the regeneration and growth problems could be mitigated to secure STY (IBIF 2004). The only way to obtain conclusive results of the experiment is to wait for 20–30 years, but rapid land use changes and heavy pressure on forests in general motivated an alternative approach that would provide a sufficient basis for effecting early changes to forest policies and on-the-ground management practices. The main alternative to waiting decades is to project the likely outcomes of the experiment via simulation modeling. The

principal assumption with this approach is that the medium- to long-term consequences of the management treatments can be projected with reasonable confidence.

It is difficult to model the dynamics of tropical forests because of their high species diversity, uneven-aged structure, and spatially heterogeneous nature (Vanclay 1994). Spatially explicit, individual-based models are most appropriate for capturing this complexity especially when the goal is to evaluate the effects of silvicultural treatments (Gourlet-Fleury and Houllier 2000, Phillips et al. 2003), which are applied to individual trees or specific ground areas (e.g., felling gaps). These models track individual trees over time either by simulating physiological processes (e.g., carbon budgets) for each tree in the stand (Ditzer et al. 2000, Huth and Ditzer 2000, Kammesheidt et al. 2001, Chambers et al. 2004), or by simulating the fundamental ecological processes of growth, mortality, recruitment, and competition (Pacala et al. 1996, Gourlet-Fleury and Houllier 2000, Phillips et al. 2003, Phillips et al. 2004b, van Ulf 2004, Arets 2005). The physiological process models require detailed site- and species-specific information about photosynthesis, respiration, and decomposition, which are unavailable in Bolivia. In contrast, models that simulate ecological processes rely on permanent plot data, which were available. I chose to use the SYMFOR modeling platform (Phillips et al. 2003, Phillips et al. 2004b) because it provides a framework to simulate these processes on a spatially explicit, individual tree basis. In addition, the ability to use, modify, and add management scenarios (van Gardingen et al. 2003) allows comparisons among the likely outcomes of the different silvicultural treatments and for assessing trade-offs between timber production and other forest values (e.g., carbon sequestration).

Using SYMFOR, I aimed to address the following research questions in this chapter:

- How effective were the applied silvicultural treatments in sustaining timber yields?
- How do forest structure and composition of change in response to different management treatments?
- How do future timber harvest volumes differ in response to each management treatment?
- How sensitive is the model to parameters for which there are little or no data?
- How reliable are the model's projections?

An additional goal of the model developed in this chapter was to provide a basis for elucidating the trade-offs between timber production and carbon sequestration, which is a major focus of Chapter 3.

Because the model was based on data spanning only 3 years, I limited my projections to 62 years with 3 harvest entries beginning in year 0 and a 30-year cutting cycle. Although the limited data for model calibration injects considerable uncertainty in the estimates, the study provides a first approximation of the likely impacts and effectiveness of the silvicultural treatments applied.

Methods

My main purpose in this chapter was to answer practical management questions rather than to develop a new or more sophisticated model. Thus, I only briefly describe the version of SYMFOR used; additional details are available in Phillips et al. (2002, 2003, 2004b) and at www.symfor.org.

Site and Data Source

Study site

The data to calibrate the model used in this study came from a 100,000 ha timber concession operated by Agroindustria Forestal La Chonta Ltda. in Guarayos Forest Reserve (15°45'S, 62°60'W) in the Bolivian lowlands (200–400 m.a.s.l.). Although the Holdridge classification system classifies the concession (hereafter La Chonta) as subtropical humid forest, La Chonta is situated in a transitional zone between wetter forests to the north and drier forests to the south and southeast. The dominant species include Ficus boliviana, Hura crepitans, and Pseudolmedia laevis, but species common in drier forests are also present (e.g., Centrolobium microchaete, Chorisia speciosa, and Aspidosperma rigida). Mean annual temperature is ~24.5°C and mean annual rainfall is ~1,500 mm, 77% of which falls between November and April. For stems with dbh \geq 10 cm the mean density is 358 \pm 8 trees/ha and mean basal area is 21.1 \pm 0.7 m²/ha (IBIF 2004). The average canopy height for trees with dbh \geq 40 cm is 28.0 \pm 0.2 m with emergent trees reaching heights of 50 m (IBIF 2004). The forest is extremely fire prone for about 130 days/year (Chapter 1); in 1995, 30% of the concession burned (Pinard et al. 1999), and a 1999 fire destroyed the town adjacent to the concession. Nevertheless, there were no signs of recent fires in my study area. Soils are moderately fertile inceptisols and 10–15% of the area has black anthrosols (Paz 2003).

La Chonta typically harvests 10–12 tree species and 7–20 m³/ha (3–5 trees/ha). Harvest activities are planned based on a 30-year cutting cycle and implemented in accordance with Forest Stewardship Council principles and criteria. The minimum

diameter for felling (MDF) set by law is 70 cm for H. crepitans and F. boliviana, and 50 cm for all other species. Twenty percent of trees > MDF are left as seed trees.

Experimental design and silvicultural treatments

A silvicultural experiment in La Chonta was established in 2001 as part of a multi-site long-term silvicultural research project (LTSRP, IBIF 2004). In La Chonta, the LTSRP applied four management treatments of increasing intensity: “control” = no logging; “normal logging” = standard planned logging according to the stipulations of the Bolivian forestry law with no other silvicultural interventions; “improved management” = “normal logging” with liberation of future crop trees from vines and overtopping non-commercial trees; and, “intensive management” = “improved management” with double the harvest intensity (as measured by number of trees harvested), additional future crop tree liberation, and soil scarification in selected felling gaps. The improved and intensive treatments aimed to promote the regeneration and growth of commercial timber species, most of which are light-demanding (Mostacedo and Fredericksen 1999, Pariona et al. 2003). Evidence for the potential benefit of soil scarification on commercial regeneration was particularly strong: Fredericksen and Pariona (2002) found that Schizolobium amazonicum densities were nearly 10 times higher and height growth was twice as great in scarified vs. unscarified felling gaps.

Treatments were replicated in three blocks, each situated in a different annual harvest unit, and were randomly applied to 27 ha plots in each block (3 blocks × 4 treatments = 12 plots. (A map of La Chonta and block layout is available at: http://www.ibifbolivia.org.bo/ESP/estaciones_de_campo/la_chonta.htm). All trees ≥ 40 cm dbh were identified, tagged, measured, and mapped in these large plots. Smaller trees were censused in sub-plots nested within each large plot; trees ≥ 20 cm dbh were

measured in 13-ha subplots and trees ≥ 10 cm dbh were measured in four 1-ha plots.

Data to calibrate the model came from the first 3 annual censuses in blocks 2 and 3 (2001 to 2003). Data collected over the same period in block 1 were used for model testing. In simulations, I used 15 of the 32 available 1-ha plots from blocks 2 and 3.

Model Description and Calibration

SYMFOR overview

SYMFOR is a strategic modeling framework that allows managers to simulate and compare different forest management scenarios (Phillips et al. 2003, 2004b). SYMFOR's ecological model consists of linked sub-models for competition, growth, mortality, and recruitment that act on individual trees in annual time steps to simulate the spatial and temporal dynamics of the forest (see Figure 2-1 for model overview and flow). The SYMFOR model I used assumes a homogeneous abiotic environment. In this study, the effects of liana infestation were included as a modifier of growth, mortality, and recruitment. I used the La Chonta data to calibrate these models (see Appendix A for a list of the parameters used in this version of SYMFOR and their symbols). Separate management models simulated treatments (i.e., harvest or kill trees, cut lianas, and scarify soil) applied in the LTSRP in La Chonta (IBIF 2004). Although La Chonta is quite fire prone, I did not explicitly include fire risk or the ecological effects of fire in the model to keep it tractable and focused on the likely outcomes of the silvicultural treatments.

Ecological models

Species grouping. The purpose of aggregating species into ecological groups was to retain as much of the variation in forest dynamics as possible to allow realistic simulations while creating a tractable model by assuming that all members of a group

behave similarly in terms of growth, recruitment, mortality and response to competition. I aggregated the 153 non-palm tree species (≥ 10 cm dbh) found in La Chonta into 8 ecological groups in 3 steps using the same approach as Phillips et al. (2002). First, species with at least 25 valid growth records were grouped using cluster analysis (SAS 9.0) based on the 75th percentile of the growth rate (for each species), the maximum height of the species, and the proportion of juvenile trees (10–20 cm dbh) growing in high light. Second, using the same variables as those used in the cluster analysis, I performed a discriminant analysis to assign the remaining (rare) species to one of the 7 groups obtained from the cluster analysis.

The third step involved peer-review of the groups by forest ecologists familiar with the species in La Chonta. This step led us to shift 6 species between groups and also to split the shade-tolerant canopy group into fast- and slow-growing species. The final species grouping is shown in Table 2-1. I excluded palms, which comprise only 2.5% of all stems in La Chonta, due to lack of data to adequately model their growth, mortality, and recruitment.

Utility groups. SYMFOR uses utility groups, a second kind of species grouping, to distinguish which species within a species group (SG) are commercial, potentially commercial, and non-commercial. Although utility groups are used during the simulation of management treatments, they are assigned by the user in the input data and subsequently assigned to new trees during recruitment (see Recruitment and Management Models for further details).

Competition. Competition among trees for resources (light, water, nutrients, and space) was represented by a competition index (C_i) following the approach of Phillips et

al. (2003, 2004b). The index for each individual is based on the dbh of, and distance to, larger diameter neighbors that were assumed to be taller:

$$C_i = \sum_{j=1}^n \frac{D_j}{D_i d_{ij}}, \quad [2-1]$$

where D_i is the dbh (in cm) of the focal tree, D_j is the dbh of a neighbor (within a radius of 20 m of tree i), $D_j \geq D_i$, and d_{ij} is the distance (in m) between a focal tree i and neighbor tree j . C_i was calculated for each tree in the original data set using Eq. 2-1; values for C_i ranged from 0.0001 to 20.98 with a mean of 2.48 ($n=27,079$). C_i tends to decline with dbh because big trees are less likely to be overtopped. Although different species experience and respond to competition differently, no data were available to calibrate a species-group specific model as was done by Arets (2005) for a version of SYMFOR for Guyanese forests. Thus, for this model, I assumed that the relationship between C_i and dbh would be the same for all species groups. I modeled the dependence of C_i on dbh using non-linear regression (SAS 9.0) as a negative exponential function:

$$\hat{C}_i = a_0 \cdot e^{(a_1 \cdot D)}, \quad [2-2]$$

The estimated parameter values were: $a_0 = 28.0$ and $a_1 = -0.115$; the associated R^2 was 0.82. A dbh-independent competition index (C) was obtained—by subtracting \hat{C}_i from C_i —and used to model growth (see below). By using C , which is independent of dbh, both dbh and competition could be included in the growth model.

Growth. Growth (i.e., dbh increment) was modeled for each species group using non-linear regression (SAS 9.0) as a function of each tree's dbh, its competition index, and whether or not it carried lianas:

$$I = [D(p_0 L + 1)] \cdot [(p_1 + p_2 \cdot e^{(p_3 D)}) + p_4 C + p_5], \quad [2-3]$$

where I = estimated annual dbh increment (in cm/yr), p_0 – p_5 are estimated parameters for each species group, C is the diameter-independent competition index, and L is the liana infestation class (0=no lianas; 1 = lianas). Equation 2-3 is similar to growth functions used in previous SYMFOR models (e.g., Phillips 2004b).

The justification for including lianas, despite lack of data on their dynamics, was that 60% of the trees in the forest were liana-infested. In addition, these trees grew substantially slower than liana-free trees: mean growth in mm/yr for trees with lianas was 3.0 ± 0.0 (n=14,872) vs. 4.9 ± 0.1 (n=9,797) for liana-free trees.

The parameters were calibrated from the averages of valid growth records between census year 0 and census year 2. ‘Valid growth records’ were those within 4 standard deviations of the mean growth rate for the species after removal of extreme outliers (e.g., > 7.5 cm/yr or < -1 cm/yr). This process of identifying valid growth records for analysis is similar to that used by Condit et al. (2004). After selecting only those trees with valid growth records, the final calibration dataset (n=19,634) still contained some individuals (n = 1,554) with negative growth. Negative growth observations result from uncertainties in the dbh measurement process and should be included in the dataset because they’re equally as valid as overly positive growth observations (Condit et al. 2004). Thus, all individuals in the final calibration dataset were included in the regression model above. (Eq. 2-3), which yielded positive growth values for all diameters (Figure 2-2).

Considering the large variation in the growth data (Figure 2-2) and the variation in competition experienced by different trees, it was no surprise that the fitted model only explained 4.8 to 11.3% of the overall variance (Table 2-2). These R^2 values are similar to those reported for growth models in other tropical forests (e.g., Gourlet-Fleury and

Houlier 2000, Phillips et al. 2004b, Arets 2005). The fitted model explains a higher proportion of the variance (range: 26 to 86%, Table 2-2) in the observed mean growth rate for each dbh class. This second R^2 was computed as follows:

$$R^2 = \frac{\sum (I_p - I_o)^2}{\sum (I_o - I_m)^2}, \quad [2-4]$$

where for each dbh class and species group, I_p is the predicted growth rate, I_o is the observed growth rate, and I_m is the overall mean growth rate for each species group.

Mean growth rates predicted by the model for liana-free trees ranged from 23 mm/yr for understory species to 92 mm/yr for intermediate-lived pioneers. Predicted mean growth rates for liana-infested trees were, on average, 41% lower than for liana-free trees, which was similar to the 43% average slower growth observed in the data.

The calculated regressions yielded parameter values that caused growth rates to continue increasing with dbh for the two shade-tolerant species groups (Table 2-2, Figure 2-2) due to a relative lack of observations at large dbh. This result meant that species would attain unrealistically large sizes. To ensure that tree diameters remained within the range observed in the data, I added a simple function to make growth constant for the largest trees ($D > D_{95}$, i.e., greater than the 95th percentile of the dbh distribution) in each species group by liana class (L):

$$I_{95} = p_6 L + p_7, \quad [2-5]$$

where I_{95} is the mean dbh increment (cm/yr); and p_6 and p_7 are parameters calibrated for each species group depending on the mean growth rate of each species group at D_{95} .

Recruitment. Lacking data to model regeneration, I chose to model recruitment (i.e., ingrowth) using the same approach implemented in most previous SYMFOR models (Phillips et al. 2003, 2004b, but see van Uft 2004). Because the LTSRP in La Chonta

had no records for trees smaller than 10 cm dbh, I modeled recruitment into the 10 cm dbh class. Although ontogenetic shifts in tree growth rates are likely, I had to assume that the growth rate of trees at 10 cm dbh was similar to the growth rate for smaller trees because I lacked growth data for smaller trees.

The recruitment model simulates ingrowth of new trees into the 10 cm diameter class annually as a function of the predicted growth rate (i.e., Eq. 2-3) of a 10 cm tree of each species group in each 10 m × 10 m grid square in the simulated stand. SYMFOR calculates the predicted growth rates for potential new recruits (=10 cm dbh) by species group based on the average competition index for each corresponding grid square. The predicted growth rates, in turn, determine the probability of ingrowth.

I considered several ingrowth probability models, but chose an exponential function because it was the only model that did not cause extirpation of any of the species groups in 60-year test simulations. I assumed that no species group would be completely eliminated from La Chonta during such a short period of time. A second justification for using this model was that functions with similar form were used in previous SYMFOR models (Phillips et al. 2003, van Uft 2004, Arets 2005). I calibrated the selected function with a weighted non-linear regression fitted to the ingrowth data (IBIF 2004):

$$F_j = i_1 \cdot e^{(i_2 I_m)}, \quad [2-6]$$

where for each species group j , F_j is the probability of recruitment, i_1 and i_2 are estimated parameters, and I_m is the mean growth rate of 11 growth rate classes (corresponding to different levels of competition) for each species group. The weighting factor was the number of grid squares with recruits.

The fitted model explained 23.4 to 91.3% of the variance for 6 of the 8 species groups (Table 2-3), but explained only 12.2% of the variance for the intermediate-lived pioneers and only 0.9% of the variance for the colonizing pioneers (Table 2-3, Figure 2-3). The recruitment probabilities predicted by the model for most species groups ranged from 0.1% per year (at high competition for dry forest species) to 7.5% per year (at low competition for slow-growing shade-tolerant species). Recruitment rates for the dry forest and light-demanding species were an order of magnitude lower than rates for the other species groups.

In this and most previous versions of SYMFOR, it is assumed that disturbances (treefall gaps, skid trails, scarified areas, and liana tangles) kill advanced regeneration in the affected grid squares. Recruitment only occurs in these grid squares once the age of the disturbance equals the time required for a newly established seedling of each species group to reach 10 cm dbh. Obviously, many factors influence this ‘ingrowth time’ (T_i), and ideally T_i would be estimated from actual data from all stages of regeneration. Lacking these data, I estimated T_i based on the maximum growth rates of juvenile trees (dbh \leq 20 cm) in the dataset (Table 2-3).

To simplify the model, recruits were assumed to be liana free. Upon recruitment, the annual probability that a tree will become liana infested was based on its species group and the liana load in its neighborhood (see section on lianas below).

SYMFOR assigns a utility group to each new recruit to indicate whether it is commercial, potentially commercial, or non-commercial, and also whether its dbh must be 50 cm or 70 cm before it may be harvested. For each species group, the probability a recruit will be assigned a particular utility group equals the proportional representation of

that utility group in the input data (see Management Models and Tables 2-13 and 2-14 for additional details).

Natural mortality. Previous SYMFOR models have calibrated mortality based on the assumption that un-logged forest is at dynamic equilibrium (Phillips et al. 2003). This approach assumes that the number of tree deaths necessary to maintain a stable dbh distribution equals the mortality rate for each dbh class (Phillips et al. 2003, 2004b). Given the structure and composition of the forest in La Chonta, it is unlikely that it is at dynamic equilibrium and therefore modeling mortality to mimic that state seems unjustified. Instead, I modeled mortality as a function of each tree's dbh, species group, and liana class. Because there was no reliable way to distinguish 'natural' mortality from logging related mortality, I restricted the dataset to the control treatment. Of the 6,618 trees in this restricted dataset, 273 died 'naturally' over a period of 1.9 years yielding an annual mortality rate of 2.2%. Although using only a subset of the database further reduced the limited data available for calibration of a mortality model, using the data from the logging treatments probably would have biased 'natural' mortality rates upward.

I fit a logistic regression (SAS 9.0) to the data with tree status (live or dead) as the dependent variable and species group, dbh, and liana class (L) as predictors. Of the possible interactions among these factors, I found that only dbh \times liana class was significant. Thus, the resulting model for the linear predictor of the logistic regression (M_p) was:

$$M_p = m_1 + m_2D + m_3L + m_4D \cdot L, \quad [2-7]$$

where m_1 – m_4 are parameters estimated by the regression (Table 2-4). I obtained the annual probability of mortality (M) by transforming M_p from the logit scale and accounting for the time interval between censuses as suggested by Alder (1995):

$$M = 1 - \left[\frac{1 - e^{M_p}}{1 + e^{M_p}} \right]^{\left(\frac{1}{t}\right)}, \quad [2-8]$$

where $t = 1.9$ years (i.e., the mean interval between the first and third censuses for the entire dataset).

The goodness of fit of a logistic regression model is indicated by the residual deviance, degrees of freedom, and scaled residual deviance (which equals the deviance divided by degrees of freedom). The residual deviance was 2,193 for 6,607 degrees of freedom yielding a scaled residual deviance of 0.33 for the fitted model.

The average annual mortality rates predicted by the model for liana-free trees ranged from 1.9% for slow-growing shade-tolerant species to 7.8% for colonizing pioneers, and for liana-infested trees ranged from 3.1 to 13.1% for the same species groups respectively (Figure 2-4). Liana-infested trees had predicted mortality rates 61% (range: 30–105%) higher than liana-free trees across all species groups and diameters (Figure 2-4).

In previous SYMFOR models, it was necessary to introduce a supplemental mortality function to ensure that large trees would eventually die. I introduced a similar function to calculate the annual mortality (M') for trees of each species group and liana class where $D > D_{95}$:

$$M' = m_{95i} + \left(\frac{(D - D_{95i}) \cdot (m_5 - m_{95i})}{D_{\max i} - D_{95i}} \right) \cdot \omega_i, \quad [2-9]$$

where for each species group i , D_{95i} is 95th percentile of the dbh distribution, D_{maxi} is the maximum observed dbh, ω_i is the ratio of the wood density of the colonizing pioneers to the wood density of each of the other species groups, and m_{95i} is the probability of mortality at D_{95i} . The parameters for m_{95i} were determined by

$$m_{95} = m_6L + m_7, \quad [2-10]$$

where m_6 and m_7 are parameters (Table 2-5) calculated from the mean value obtained from Eq. 2-8 for trees of each species group and liana class with $D > D_{95}$. The parameter m_5 is a user-defined value that I varied from m_{95i} to 1 during model evaluation. Annual mortality was constant (i.e., it equaled m_{95}) with $m_5 = m_{95}$. The amount of additional mortality beyond m_{95} was a function of m_5 ; M' increased as m_5 approached 1. Thus, for simplicity later in this paper, I refer to m_5 as the ‘supplemental mortality parameter’. In initial simulations, it was apparent that the colonizing pioneers especially were growing to unrealistic sizes. The purpose of the wood density ratio parameter (ω_i) was to ensure that colonizing pioneers and other species groups with low wood densities would be more strongly affected by this supplemental mortality function than species groups with higher wood densities.

Damage mortality. I lacked data to determine what proportion of tree deaths were due to natural tree falls or falling branches vs. other causes of mortality (e.g., disease), which meant that the parameter estimates for Equations 2-7 to 2-10 included both causes of mortality. Because SYMFOR accounts for damage-related mortality separately (see Phillips et al. 2003 for details), it was necessary to adjust the value of M and M' in Equations 2-8 and 2-9 downward so that they represented only non-damage caused

mortality. Specifically, I multiplied M (or M^{\wedge}) by $(1-m_d)$, where m_d is a parameter that I varied during model evaluation from 0.03 to 0.20.

In SYMFOR, trees can either die standing or falling as determined by the parameter P_f (the probability of falling). If they die standing, SYMFOR assumes that they do not kill other trees. If they fall when they die, they may kill trees in their path with probability P_d . The damage adjustment parameter, m_d , is the product of these probabilities ($P_f \cdot P_d$). I lacked data to calibrate these parameters; hence, their values were best estimates subsequently tested in the sensitivity analysis (see below).

Liana class and assigning a liana class to recruits. Lianas are common in La Chonta and a significant challenge for managers (Alvira et al. 2004). Lacking adequate data on liana dynamics, however, the simulation of lianas had to be approximated from field observations, the literature, and logic. Thus, lianas are simulated either as attributes of trees by a liana class variable (0=no lianas; 1=lianas), or as infestations of tree fall or felling gaps (i.e., liana tangles), which delay recruitment for 9 to 62 years depending on the species group.

The liana class, L , of existing trees in the stand was obtained from field data. I assumed that L never changes from 1 to 0 except by liana cutting (a silvicultural treatment), whereas trees without lianas (whether existing at the beginning of the simulation or new recruits) can become infested with probability = 0.0475 annually until 60% of the trees in the stand are liana infested. I estimated the annual probability of infestation and proportional limit from data available on liana class in La Chonta (IBIF, unpublished data; see Appendix B for details).

All recruits enter the stand without lianas, but depending on their species group and neighborhood (i.e., within 20 m of the recruit), they may become liana infested. The probability that a recruit might become liana infested is defined by a single parameter that varies for each species group according to the proportion of liana-infested neighbors. The parameter values were obtained from the proportion of liana-infested juvenile trees ($D < 15$ cm) in the data for each species group in each of four neighborhood infestation classes (Table 2-6).

Liana tangles. The many liana infested gaps and other areas of La Chonta without advanced tree regeneration constitute a major challenge for managers because they reduce the future timber value of the forest stand. In general, the recruitment of commercial trees is delayed in these low productivity areas due to high liana densities (Schnitzer et al. 2000) as well as monodominant patches of clonal herbs (e.g., Heliconia spp.) or treelets, especially chocolatillo (Erythrochiton fallax). Lacking data on the dynamics of any of these areas of arrested succession, I assumed that they would all delay tree recruitment in a similar way, and hence considered them all to be ‘liana tangles’ in which a tree could not recruit until the age of the liana tangle equaled the ingrowth time (T_i) estimated for each species group (Table 2-3). At that time, the basic recruitment rules described above applied.

I spatially represented these liana tangles in SYMFOR through their specific association with tree fall gaps whether inferred from the input data or created during simulations. To create liana tangles from the input data, I instructed SYMFOR to randomly sample $10\text{ m} \times 10\text{ m}$ areas without trees > 10 cm dbh. Based on the observation that half of the 1-year old felling gaps I evaluated had 50% or more liana

cover (GB unpublished data, Alvira et al. 2004), SYMFOR then randomly creates a liana tangle in half of those areas. Finally, I assumed that liana tangles would remain as such for up to 20 years, and therefore assigned an age (1–20 years) to each liana tangle from an even-aged distribution.

SYMFOR creates liana tangles in simulated treefall or felling gaps based on the liana class of the falling tree and the proportion of liana-infested neighbors (i.e., trees within 20 m of the falling tree). Without reliable data to estimate parameters for this process, I assigned the probability of a gap becoming liana infested based on a series of conditions (Table 2-7).

Other functions. SYMFOR uses several other functions to calculate key attributes of trees during the simulations, including height, volume, and biomass.

Tree height is calculated based on the allometric relationship with dbh described by Thomas (1996):

$$H = h_{\max} \left(1 - e^{(-h_1 D^{h_2})} \right), \quad [2-11]$$

where h_{\max} , h_1 , and h_2 are parameters estimated by non-linear regression for each species group. The data used to estimate these parameters comprised dbh and height measurements for 1,174 trees of 59 species in La Chonta (Poorter et al. In press). Height was measured with a clinometer (height > 8 m) or with an extension pole (height < 8 m). Although most trees in this dataset were not liana infested, I used the main LTSRP database to compare heights for trees with and without lianas. I found no significant difference, and hence decided to use the estimated parameter values (Table 2-8) for all trees regardless of liana class. SYMFOR uses tree height to calculate volume (see below) as well as the size of gaps caused by falling or felled trees.

Commercial timber volume (V) is calculated from a tree's basal area (G , calculated from dbh), a form factor (f), and its merchantable height, which is estimated by a parameter called "crown-point" (c_p) in other SYMFOR models (Phillips et al. 2003):

$$V = G \cdot c_p \cdot f \quad [2-12]$$

The form factor, f , was assumed to be 0.65 for all species groups and was taken from an analysis of a large database of trees in the La Chonta region (Dauber et al. 2000). The crown-point for each species group was calculated as:

$$c_p = H \cdot a, \quad [2-13]$$

where H (height) is calculated as described above, and a is a species group specific parameter that represents the ratio of merchantable height to total tree height. The value of a for each species group was approximated using the mean log length from harvested trees (Table 2-9).

The biomass function in SYMFOR calculates the aboveground biomass (B) of each tree (kg) annually based on its dbh (D), wood density (ρ), and total height (H) using a function calibrated by Chave *et al.* (2005) for moist tropical forest stands:

$$B = 0.0509 \cdot \rho D^2 H, \quad [2-14]$$

The values for ρ (Table 2-10) were obtained both from La Chonta (L. Poorter, unpublished data) and the literature (Chudnoff 1984).

The necromass function in SYMFOR calculates the annual change in mass of dead trees, which is an estimate of the mass of woody debris. A dead tree's biomass is reduced annually by a decay function (K_d) according to its dbh, mean wood density (ρ) for each species group, and parameters estimated by Chambers et al. (2000) for trees in the southwest Amazon:

$$K_d = (1.104 - 0.670\rho - 0.163 \cdot \log(D))^2 \quad [2-15]$$

Management models

The simulated harvests in SYMFOR target individual trees that meet selection criteria including size, stem quality, and commercial status. A utility group variable defines the commercial status of each tree within each species group. The input data contain the initial utility group information. Each tree was assigned to 1 of 4 utility groups depending on actual practice in La Chonta: 1=valuable species typically harvested in the normal treatment with minimum dbh for felling limit (MDF) = 50 cm; 2=valuable species with MDF = 70 cm; 3=species not typically harvested by La Chonta, but considered commercial or potentially commercial (and therefore harvested only in the intensive management treatment, MDF = 50 cm); and 4= non-commercial trees (Table 2-11). During the simulations, new recruits are assigned to a utility group based on the proportional composition of utility groups within each species group in the input data (Table 2-12).

I adapted existing SYMFOR management models and functions (see Phillips et al. 2003, 2004b), or created new ones, to mimic the silvicultural treatments (i.e., cutting cycle, selective felling, skidding, poison-girdling, liana cutting, and soil scarification) applied in La Chonta. For example, depending on the size and stem quality criteria for each utility group, SYMFOR simulates liana cutting by changing the liana class of infested trees from 1 to 0. Depending on dbh and proximity to future crop trees, SYMFOR also kills (via poison-girdling) non-commercial competitors (utility group 4).

I created a new model to simulate the soil scarification treatment in La Chonta, which cleared vegetation down to mineral soil in selected felling gaps at the time of tree-fall. Gaps were considered eligible for scarification if:

- No advanced regeneration of commercial species was present in the gap; and,
- At least 1 mature (dbh > 30 cm) commercial individual was present within 20 m of the gap.

If these criteria are met, the scarification function kills all non-commercial trees in the gap.

The effect of scarification on recruitment is simulated in the same way as liana tangles, skid trails, and other kinds of damage: once the age of the scarified gap equals the ingrowth time required for each species group (Table 2-3), trees of that group may recruit. Evidence from La Chonta (Fredericksen and Pariona 2002, M. Peña-Claros unpublished data), however, indicates that scarification enhances the regeneration of some species and slows the regeneration of others. To account for this differential effect, the probability of recruitment function (Eq. 2-6) is multiplied by a species group specific parameter (E_s ; Table 2-13). Depending on the species group, E_s increases, decreases, or does not change the probability of recruitment. The values for E_s are the mean relative densities of each species group in La Chonta, which were calculated by M. Peña-Claros (unpublished data) as the ratio of mean seedling density in the scarified gaps (n=81) vs. the non-scarified gaps (n=78).

Model Evaluation

Model tuning

Previous SYMFOR models were evaluated for internal and logical consistency using methods similar to those described by Vanclay (1994). Most of these models (except van Ulft 2004 and Arets 2005) assumed that the forests they were simulating

were at dynamic equilibrium. In most cases, the calibrated parameters in the functions for growth, mortality, and recruitment had to be adjusted so that the simulated unlogged forests behaved as if they were at this hypothetical steady state. I decided against this approach because it is unlikely that La Chonta is at dynamic equilibrium, and because it will be impossible to test assumption from field data for many years. In addition, even apparently undisturbed Amazonian forests have become more dynamic (cf. Arets 2005)—with increases in biomass and turnover rates—in recent decades (Baker et al. 2004, Lewis et al. 2004a, Lewis et al. 2004b, Phillips et al. 2004a).

Although I did not tune the model to behave as if it were at dynamic equilibrium, I nevertheless adjusted parameters that were either not calibrated from data (i.e., the probability a dying tree will fall; the probability a falling dead tree will kill a neighbor; the minimum dbh below which a dying tree will remain standing; and the liana infestation rates) or that had a high degree of uncertainty (i.e., the supplemental mortality for large trees; the ingrowth time; and the effect of scarification on recruitment rates). I estimated values for these parameters by evaluating the response of several key variables—total number of trees (N) and basal area (G), N and G by species group, and proportion of N that were liana-infested (N_l)—during 60-yr simulations repeated 10 times with input data from 15 of the 32 1-ha plots. I chose values that were consistent with the most reasonable expectations considering the short simulation period: no species group extinctions; liana-infested trees account for 54–60% of total N ; and, tree density, basal area, and maximum dbh for each species group remain within the range of variation observed in the data.

Model testing

Lacking long-term, independent data against which the simulation results could be compared, meaningful model testing was limited to a statistical comparison of the data used to calibrate the model (LTSRP blocks 2 and 3) with an independent dataset from the same forest (LTSRP block 1). Although less rigorous a test of a model than validation of the model's projections with time-series data, this approach nevertheless tests whether the data used to calibrate the model are idiosyncratic or representative of the forest the model aims to simulate. If the calibration data do represent the forest (i.e., the test and calibration datasets are similar), then it can be concluded that the model will behave as well for test data from different areas of the same forest as the model behaves with the calibration data.

Thus, I tested for differences between the calibration and test datasets in terms of:

- Growth rates (mean and 95th percentile of the distribution, or p_{95}) by species group with a Wilcoxon 2-sample test;
- Number of new trees by species group as a proportion of initial tree densities using Poisson regression with a log link function; and,
- The proportion of total N and total basal area by species group, and the proportion of all trees that were liana-infested using general linear models after arcsine-square-root transforming the proportions.

I obtained means and / or proportions for these variables for each of the 1-ha plots in the experimental blocks ($n=32$ for calibration dataset; $n=16$ for test dataset).

Model sensitivity to parameters not calibrated from data

Assessing the sensitivity of the model's behavior to changes in the values of parameters estimated from the calibration data was beyond the scope of this chapter.

However, I wanted to determine how sensitive the model was to the variables for which

the calibration was either highly uncertain (due to limited data) or simply based on best estimates (see Table 2-14). The tested parameters were in functions that determined:

- Supplemental mortality of large trees;
- Liana infestation rate;
- Damage related mortality; and,
- Recruitment after silvicultural treatments.

The damage parameters included the minimum dbh of a falling dead tree, the probability that a dead tree will fall, and the probability that a falling dead tree will kill neighbors in its path.

Because I could not determine the uncertainty associated with the tested parameters, I simply increased or decreased (by 50% of the baseline) each value during sensitivity analyses (Table 2-14). I also ran simulations to test the effect of additional deviations in the values of the parameters for supplemental mortality (m_5) and liana infestation rate (Table 2-14).

Rather than set the supplemental mortality parameter (m_5) to the same value for all species groups in the baseline scenario, I set it higher for the colonizing pioneers to ensure that they would die before reaching unrealistic diameters. My justification for this decision was the observation that colonizing pioneers especially grew to unrealistic sizes in preliminary simulations with values of m_5 lower than 0.2. In contrast, the diameters of trees in the other species groups appeared to stay within the range observed in the data in 60-year simulations with $m_5 = 0.05$. Thus, I used these values for m_5 in the baseline scenario of the sensitivity analysis.

Overall, I ran 17 simulations with the control (no logging) treatment for the parameters listed in Table 2-14. I ran an additional 6 simulations for the two recruitment parameters (T_i and E_s) that could be influenced by silviculture; I used the intensive

management treatment for these simulations. The simulations for liana infestation rate and the two recruitment parameters were run for 60 years. All other simulations were run for 120 years. The input data for the simulations consisted of 15 of the 32 available 1-ha plots from the calibration dataset. I repeated simulations of each of the plots 10 times.

I evaluated the model's sensitivity in terms of the response variables mentioned above: total N and G , N and G by species group, and N_l . For liana infestation rate, I also examined the number of years required to reach the stand liana threshold (60%). I calculated sensitivity (S) according to the formula provided by Vanclay (1994):

$$S = \frac{\partial v / v}{\partial \beta / \beta}, \quad [2-16]$$

where $\partial v / v$ is the relative change in the result variable and $\partial \beta / \beta$ is the relative change in the parameter value.

Comparison of treatment impacts

I compared the management treatment impacts using the same response variables mentioned above: total N and G as well as N and G by species group, and N_l . Using the parameter set indicated in Tables 2-1 to 2-14, I ran simulations of each management treatment for 62 years, which was long enough to evaluate the impacts of two cutting cycles and to estimate potential yield from a third harvest entry. I used 15 of the 32 available 1-ha plots from the calibration dataset for input and repeated simulations for each plot 15 times.

Results

Model Testing: Comparing Test vs. Calibration Data

Growth rates

Growth rates (both means and p_{95}) were similar between the calibration and test datasets for all species groups except the dry forest species. For dry forest species, mean growth was higher in the calibration dataset than in the test dataset ($Z_{15,31} = -2.1$; $P = 0.04$). The 95th percentile of the growth rate distribution, however, did not differ for this species group between the datasets.

Recruitment

The Poisson regression indicated that the calibration and test datasets differed in per capita recruitment ($\chi_1 = 9.5$; $P = 0.002$). The per capita recruitment of colonizing pioneers (SG7), in particular, was greater in the calibration than in the test dataset ($\chi_1 = 21.5$; $P < 0.001$). In contrast, per capita recruitment was on average 59% greater (range: 4–116%) in the test dataset than in the calibration dataset for all other species groups (Table 2-15). The explanation for these differences is not immediately obvious but could be attributable to various factors including, environmental differences among the experimental blocks, differences in the way the management treatments were applied in each block, and unusually high or low recruitment rates for the years sampled in one of the blocks.

These results led me to run two test simulations, one with the recruitment parameter values doubled for all species groups except the colonizing pioneers, and the second with the recruitment rate halved for colonizing pioneers and left unchanged for all other species groups. The outcome of the first test was unrealistic: total N and total G increased by 40–50% over 60 years. The outcome of the second test, in contrast, seemed

reasonable: total N and total G increased only slightly over 60 years. Moreover, the density and basal area of the colonizing pioneers remained fairly constant over 60 years, whereas this species group doubled in density and basal area when the unadjusted (i.e., parameterized) recruitment rate was used in test simulations. This latter behavior of the model was counterintuitive and inconsistent with successional theory, which predicts that in the absence of disturbance, short-lived colonizing pioneers should not increase in relative dominance. Thus, I used the adjusted parameter value for colonizing pioneers in subsequent simulations.

Forest structure comparison

Tree density, basal area, and dbh distribution. The calibration and test datasets appeared similar upon visual inspection of their dbh distributions, but they differed in terms of mean dbh and mean basal area. Specifically, the mean dbh in the calibration dataset ($n = 32$) was 1 cm greater than in the test dataset ($n = 16$): 22.3 ± 0.15 vs. 21.3 ± 0.17 cm ($t_{46} = 2.9$; $P = 0.006$; Satterthwaite method for unequal variances). The 95th percentile of the dbh distribution was also higher in the calibration (51.3 cm) than in the test (45.6 cm) dataset. Consequently, basal area was greater in the calibration than in the test dataset (21.1 ± 0.7 vs. 19.1 ± 0.5 m²/ha; $t_{46} = 1.94$; $P = 0.02$; Satterthwaite method for unequal variances). Densities (#/ha) of trees ≥ 10 cm dbh in the two datasets were not significantly different (calibration: 358.1 ± 8.2 ; test: 384.2 ± 9.1 ; $t_{46} = -1.97$; $P = 0.06$). Although the mean dbh and basal area of the two datasets statistically differed, I concluded that they were biologically similar because of the small magnitude of these differences and because the overall tree densities were similar. This conclusion was further supported by the following two tests.

Species group composition. Overall, the calibration and test datasets did not differ in terms of species composition ($F_{1,366} = 0.02$; $P = 0.9$), although the understory and long-lived pioneer species groups were more abundant in the calibration dataset than in the test dataset ($F_{7,366} = 176.4$; $P = 0.001$; Table 2-16). Similarly, the proportion of total basal area was similar in the two datasets ($F_1 = 0.34$; $P = 0.56$).

Liana infestation. The proportion of trees that were liana infested when the plots were established (i.e., census 1) was similar in the calibration and test datasets. The proportion of all trees without lianas in the test dataset was 48% and in the calibration dataset was 44% at census 1. At census 3, those proportions dropped to 43% (test) and 42% (calibration).

Summary. Despite differences between the test and calibration datasets in per capita recruitment and some differences in forest structure, the results of the other tests suggest that the datasets are similar. Thus, I concluded that the calibrated model would perform equally well using any input data from La Chonta or similar forests.

Model Sensitivity to Parameters not Calibrated from Data

Mortality of large trees: total tree density and basal area

Total tree density (total N) was relatively insensitive ($S = 0.01$) to changes in the supplemental mortality parameter (m_5) within the range of values tested ($m_5 = m_{95}$ to 0.1 for non-colonizing pioneers and m_{95} to 0.3 for colonizing pioneers). Total N decreased, as expected, with higher values of m_5 , but the change relative to the baseline was small (Figure 2-5a). When m_5 was doubled for all species groups (except the colonizing pioneers) total N differed by <1% after 120 years between the baseline (359 ± 3 trees/ha) and test scenarios (357 ± 2 trees/ha). Without supplemental mortality (i.e., $m_5 = m_{95}$), total N increased by only 3% ($S = 0.68$).

Total basal area (G) was somewhat more sensitive to changes in m_5 than total N (Figure 2-5b). Total G decreased by 1.6 m²/ha (7%; $S = 0.14$) from 24.0±0.2 in the baseline to 22.2±0.2 m²/ha when m_5 was doubled (compare baseline vs. s2 and s5 in Figure 2-5b). When $m_5 = m_{95}$, total G increased by 10% ($S = 1.97$, Figure 2-5b).

Mortality of large trees: N and G by species group

Tree density was unaffected when m_5 was doubled, and also remained similar to the baseline for most species groups with $m_5 = m_{95}$ (Table 2-17). This response variable was most sensitive to setting $m_5 = m_{95}$ in the colonizing pioneers (SG7), the long-lived pioneers (SG2), and slow-growing shade-tolerant species (SG3). Tree density for the colonizing pioneers increased by 12% ($S=0.12$), for the long-lived pioneers decreased by 8% ($S=0.15$), and for the slow-growing shade-tolerant species increased by 7% ($S=0.15$; Figure 2-6a).

As expected, basal area was somewhat more sensitive to changes in m_5 for most species groups, although for many groups the changes were quite modest (Table 2-17). Doubling the value of m_5 caused less than a 10% change in basal area for all but three species groups (Figure 2-6b): intermediate-lived pioneers (decreased 23%), colonizing pioneers (increased 11%), and fast-growing shade-tolerants (decreased 18%).

The effect on G was greater for most species groups when $m_5 = m_{95}$. The most sensitive group was the fast-growing shade-tolerant species, which increased in basal area by 26% with $m_5 = m_{95}$. The intermediate-lived pioneers and colonizing pioneers both increased in basal area by 20% and the dry forest species group increased by 19%.

Mortality of large trees: maximum dbh

Within the range of values of m_5 tested (m_{95} to 0.1), maximum dbh at year 60 of the simulation was virtually identical for the non-colonizing pioneer species groups. Thus, I decided to keep the value of m_5 at 0.05 for the other simulations.

Liana infestation

The calibrated value of liana change probability, which controls the annual rate of liana infestation of liana-free trees, was 0.0475 (see Appendix B for calculation). None of the tested response variables was sensitive to changes of up to 100% in the value of this parameter. The time required for the proportion of trees with lianas to reach the threshold value of 60% (from the mean value of 54% in the input data) depended on the value of this parameter. That threshold was reached within 10 years with the baseline value and within about 60 years with a value of 0.02. Because the impacts on tree density and basal area were negligible, I used the baseline value (from Appendix B) in further simulations.

Damage related mortality

Total tree density and basal area were relatively insensitive to changes of 50% in the parameters controlling damage-related mortality. After 120 years, depending on which parameter was altered, the deviation from the baseline ($N = 360$; $G = 24 \text{ m}^2/\text{ha}$) was only 1–3% for total tree density (i.e., ± 10 trees) and 1–4% for total basal area (i.e., $\pm 1 \text{ m}^2/\text{ha}$). Tree density and basal area were also relatively insensitive to changes in damage-related mortality at the species group level, though these response variables increased or decreased by 6–9% for some species groups depending on which parameter was changed.

Tree density was sensitive to changes in these parameters principally for slow-growing shade-tolerant species. Reducing the probability that a tree will fall when it dies (P_f) by 50% caused an 8% increase in the number of trees per ha (from 95 ± 3 to 103 ± 4). Conversely, doubling P_f caused an 8% decrease in the number of individuals of this species group.

Basal area was somewhat more sensitive to changes in damage-related parameters than tree density for most species groups. Again, the slow-growing shade-tolerant species group was the most sensitive. Reducing the probability that a dying tree will fall by 50% caused a 7% increase in basal area in this species group (from 5.2 ± 0.5 to 5.6 ± 0.5 m²/ha) whereas doubling that probability caused a 9% decrease.

Silviculture-related recruitment

Total tree density and basal area were insensitive at year 60 to 50% changes in the values of two species group specific parameters—ingrowth time (T_i) and scarify effect (E_s)—that affect post-silviculture recruitment rates. These response variables were similarly insensitive at the species group level with one exception. When the value of T_i of each species group was decreased by 50%, the basal area of the dry forest species group decreased by 10%. When the value of T_i for each species group was increased by 50%, basal area of the dry forest species group decreased by 15%. This species group exhibited the poorest recruitment in the dataset.

Summary

In general, the model did not appear to be particularly sensitive to any of the parameters that were calibrated with little or no data. The most sensitive response variable tested was basal area, although it did not change by more than 26% under any of

the scenarios tested. Of the parameters tested, the model was most sensitive to the value for supplemental mortality.

Comparison of Treatment Impacts

Harvest volumes

Harvest volumes, regardless of management treatment, were quite low by tropical standards even in the first harvest entry. In the normal harvest treatment, only 2.4 ± 0.4 trees/ha were felled in the first cutting cycle for a mean total volume of 10.3 ± 1.7 m³/ha. In the intensive management treatment, 3.5 ± 0.6 trees/ha were felled for a mean total volume of 14.7 ± 2.4 m³/ha. These volumes are similar to the actual harvest volumes obtained in La Chonta: on average 2.3 trees/ha and 10.4 m³/ha were harvested from the normal harvest treatment and 4.0 trees/ha and 14.4 m³/ha were harvested from the intensive management treatment (IBIF, unpublished data).

Both the number of trees felled and volume harvested declined in the simulated 2nd and 3rd harvest entries (Tables 2-18 to 2-21, Figure 2-7) regardless of management treatment. In the normal harvest treatment, relative to the first cutting cycle, timber yields were only 33% in the second harvest entry and 14% in the third harvest entry. In the intensive management treatment, yields relative to the first harvest were 47% and 32% for the second and third harvest entries, respectively. While falling far short of STY, the intensive management treatment yielded 105% more timber in the second harvest entry ($t_{28} = -3.51$, $P = 0.0015$) and 231% more timber in the third harvest entry ($t_{28} = -4.70$, $P < 0.001$) than did the normal harvest treatment (Tables 2-20 and 2-21, Figure 2-7). These differences were attributable to both the greater number of species harvested in the intensive management treatment (Tables 2-20 and 2-21) and the

silviculture applied in the intensive treatment. The applied silviculture apparently increased commercial species' growth rates and recruitment compared to the other treatments (Table 2-21, Figures 2-8 and 2-9). The potentially commercial species comprised about 6% of the harvest volume in the first cutting cycle, and 15% and 28%, respectively in the second and third cutting cycles of the intensive management treatment (Table 2-21).

Effects on overall stand structure

Total tree density. The simulated management treatment effects on tree density (number of trees > 10 cm dbh / ha) were small, consistent with expectations, and similar in magnitude and direction to short-term effects observed in the field. Tree density decreased by 2.8% (from 350 ± 15 to 340 ± 5) over 60 years in the absence of harvesting or additional silviculture (Figure 2-10a). After two harvest cycles (=60 years), tree densities recovered to the same levels in response to the normal harvesting regime (327 ± 4 trees) and the intensive management treatment (326 ± 4 trees) (Figure 2-10a). After the first cutting cycle, tree density was reduced by 7.5% in the normal harvest treatment and 8.5% in the intensive management. The post-harvest silviculture in the intensive management treatment further reduced tree density by 1.5% (Figure 2-10a). Regardless of management intensity, after each of the first two cutting cycles, tree densities recovered to within 3–4% of those observed in the control treatment within 30 years (Figure 2-10a). Tree densities recovered faster in response to the intensive management treatment than in response to the normal harvest treatment implying better recruitment or lower mortality or both (Figure 2-10a).

Total basal area. The effects of the management treatments on basal area were slightly greater than the effects on tree density, which is logical considering that the

largest trees were harvested. Plot basal area increased by 8.1% (from 20.2 ± 1.0 to 21.9 ± 0.3) over 60 years in the absence of logging (Figure 2-10b). After the first cutting cycle, basal area was reduced by 15.4% (13.4% from felling and 2.0% from additional silviculture) in the intensive management treatment and by 11.1% in the normal harvest treatment. The second harvest reduced basal area by 9.8% (including silviculture) in the intensive management treatment and by 4.2% in the normal harvest treatment. By year 60 (after 2 cutting cycles) total basal area recovered to the same level as at year 0 for both harvest treatments, but was 8% less than in the control treatment (Figure 2-10b). Although more basal area was removed in the intensive management treatment than in the normal harvest treatment, the faster growth rates for commercial species afforded by the applied silviculture (Figure 2-9) apparently contributed to faster basal area recovery (Figure 2-10b).

Effects on species composition

Tree density. In the absence of logging or other silvicultural treatments, tree densities did not fluctuate dramatically for most species groups (Figure 2-11a). The greatest changes during the 60-year simulation were observed in the long-lived pioneers (29% increase), intermediate-lived pioneers (16% increase) and dry forest species (14% decrease). The change in abundance of other species groups over the 60-year period was less than 10%.

The harvest treatments amplified the patterns observed in the control plots during the 60-year period for most species groups. The most extreme examples of this observation were in the understory and slow-growing shade-tolerant canopy species. In both cases, the reduction in tree density observed in the control treatment was doubled in the normal harvest treatment and nearly tripled in the intensive management treatment.

Most other changes in the patterns observed in the control treatment were more moderate. The main differences observed with intensive management were greater increases in the long-lived pioneers and greater decreases in the slow-growing shade-tolerant canopy species (Figure 2-11a).

Basal area. Changes in basal area at the species-group level during the 60-year simulation period were greater than those observed for tree density in the control as well as in the harvest treatments (Figure 2-11b). In the control treatment, the greatest increases in basal area were in the fast-growing shade-tolerant species (105% increase) and intermediate-lived pioneers (83% increase). The basal area of the slow-growing shade-tolerant and understory species also increased by 23% and 11%, respectively. In contrast, the basal area of the light-demanding species (many of which are commercial) decreased by 35% and the basal area of the dry forest species (some of which are commercial) decreased by 18% over 60 years in the control treatment. Both of these species groups exhibited poor recruitment and slow growth in La Chonta.

The impact of the harvest treatments on basal area varied for each species group. As was the case in the control treatment, the greatest increases in basal area for both the normal harvest and intensive management treatments occurred in the fast-growing shade-tolerant species and intermediate-lived pioneers. The percentage increase in basal area, however, was less for both species groups in the intensive management treatment than in the normal harvest treatment (Figure 2-11b). Basal area of the intermediate-lived pioneers increased by 93% in the normal harvest treatment and by only 80% in the intensive management.

The silviculture applied in the intensive management treatment appeared to benefit the principal commercial timber species groups. The intensive management treatment increased the basal area of the long-lived pioneers by 3% over 60 years whereas basal area of this species group decreased by 6% in the normal treatment. Also, the decrease in basal area of the light demanding species caused by intensive management was similar to the decrease observed in the control treatment, whereas the basal area of this species group decreased a further 6% in the normal harvest treatment (Figure 2-11b).

Silvicultural effects of the intensive management treatment

The intensive management treatment simulated three silvicultural treatments: liana cutting on future crop trees (FCTs), killing competitors near FCTs, and soil scarification in felling gaps. In the simulations, lianas were removed from 23–26 crop and FCTs per ha, and 6 FCT were released from neighboring competitors (Table 2-22). Depending on the cutting cycle, 37–41% of felling gaps were scarified (Table 2-22).

Liana cutting and liana infestation. The liana cutting treatment applied principally to FCTs in the intensive management treatment decreased the proportion of trees with lianas (Figure 2-12), which, together with the liberation and scarification treatments (Table 2-22), benefited the commercial tree species. During the first cutting cycle, the liana cutting treatment decreased the proportion of all trees that were liana-infested by 20% (from 54% to 43%) and also decreased the proportion of liana-infested basal area by 42% (from 64% to 37%).

Effects on growth rates. Mean growth rates (pooled across species groups, repetitions, plots, and simulation years) were about the same regardless of treatment. However, growth rates were twice as great for liana-free trees as they were for liana-infested trees (50.3 ± 0.7 mm/yr vs. 26.6 ± 0.1 mm/yr in the control treatment). The

liana-cutting treatment apparently increased growth rates of the commercial species sufficiently to allow faster post-harvest basal area recovery of these species than in the normal harvest treatment (Figures 2-8 to 2-10). Immediately after the harvest and additional silviculture, commercial species grew 15–16% faster in the intensive management treatment than in the normal harvest treatment and 19–23% faster than in the control treatment. This effect persisted for about 10 years for the commercial species, after which time growth rates among the management treatments were more similar.

Discussion

Effectiveness of the Applied Management Treatments in Achieving STY

The simulated silviculture applied in the intensive management treatment clearly benefited the commercial species as demonstrated by faster growth rates, better recruitment, and faster post-harvest basal area recovery relative to the normal harvest treatment. Consequently, compared to the normal harvest treatment timber yields obtained under intensive management were 105% greater in the 2nd harvest and 231% greater in the 3rd cutting cycle. Although neither of the harvest treatments applied in La Chonta came close to STY (at best the recoverable volume was only 47%), the intensive management treatment came closer. The timber yields obtained in the 2nd and 3rd harvests as a percentage of the volume harvested in the first cutting cycle were 15 to 20% greater in the intensive management treatment than in the normal harvest treatment.

These projections are similar to estimates of recoverable volumes (i.e., 28%) reported by Dauber et al. (2005) for a second harvest in forests like La Chonta under a management regime similar to the normal harvest treatment applied in this study except using a 20-year cutting cycle. Under their optimum scenario (which assumes growth rates of free-to-grow, liana-free trees of good form), however, recoverable volumes

approached 90% in the second cut assuming a 30-year cutting cycle. The intensive management treatment results move toward this estimate, but do not equal it because not all future crop trees were free to grow (i.e., only 6 trees/ha liberated) or remained liana-free for an entire cutting cycle, which means maximum growth rates and low mortality rates did not necessarily apply in all cases.

The projections from this study are also consistent with estimates of potential volume recovery from other Neotropical forests. In simulations of different management regimes in humid forests in Venezuela, Kammesheidt et al. (2001) estimated that 60-year cutting cycles would be required to achieve sustained yields of 30–60 m³/ha depending on the minimum felling diameter and whether conventional or reduced-impact logging were applied. In French Guiana, Gourlet-Fleury et al. (2005) estimated that only 60% of the initial stock would recover after logging with a DMC of 60 cm and a cutting cycle of 40 years. In contrast, in logged humid forests in the Eastern Amazon, Silva et al. (1995) found that the total basal area was about 75% of that in a comparable unlogged forest 13 years after logging with no additional silviculture. However, they also reported that annual commercial volume increments were only 0.8–1.8 m³ ha⁻¹ yr⁻¹ depending on whether new commercial species were included. Since their study was conducted after the removal of 75 m³/ha, the implication is that cutting cycles would need to be about 75 years to achieve sustained yields of the commercial species at the time of the first cut.

Prospects for Achieving STY in La Chonta

One of the reasons that the intensive management treatment came closer to achieving STY than the normal harvest treatment is because additional (mostly shade-tolerant) species were eligible for harvest. Although the silviculture applied in the intensive treatment yielded obvious benefits—the volume of commercial species

harvested in the 2nd cut was 74% greater under intensive management than under the normal harvest treatment—it is also important to recognize that including the potentially commercial species elevated the total yields in all three cutting cycles. In addition, the proportion of the total volume harvested comprising potentially commercial species (under intensive management) increased from only 6% in the first cut to 15% in the 2nd cut and 28% in the 3rd cut suggesting that additional silviculture will be needed to promote the growth and recruitment of the more light-demanding commercial species. Thus, although the applied silviculture helped move management toward STY, considerable work remains to achieve it in these forests if cutting cycles are to remain as short as they are at present or unless markets are found for the potentially commercial species.

Considering the relatively slow growth rates and poor recruitment of the commercial species and the short cutting cycle, it is no surprise that recoverable volumes in the second and third harvests were so much lower than in the first. The first harvest of previously unlogged tropical forests includes a subsidy from nature and the second harvest typically comprises trees that were too small to be cut at the time of the first harvest (Dawkins and Philip 1998). But, this point assumes that there is an adequate stocking of commercial trees that will reach the minimum diameter for felling (MDF) within the cutting cycle period.

Dauber et al. (2005) indicated that of the lowland forest types in Bolivia, those in the La Chonta region have the best stocking of future crop trees capable of reaching the DMC within 30 years under optimal conditions. Under such conditions, they found that

90% of the volume harvested in the first cut could be recovered in the second. The data from La Chonta, however, are less optimistic.

In La Chonta, before logging, commercial species comprised only 15% of all trees (and 11% of the total basal area) capable of attaining the MDF (50 cm) within 30 years (i.e., $\text{dbh} > 20 \text{ cm}$) under optimal conditions. Furthermore, they comprised only 9% of recruits ($\text{dbh} < 20 \text{ cm}$), which under similarly ideal conditions could be considered future crop trees for the 3rd cut. If potentially commercial species are included, those percentages increase to 50% of potential FCTs (and 75% of basal area) for the 2nd cut and 32% of trees (and 36% of basal area) for the 3rd cut. These percentages improved only slightly under intensive management.

An obvious research question that emerges from this study is the extent to which more intensive management strategies would come closer to achieving STY. The model described in this study could be used to evaluate the effectiveness of various alternatives. Although the simulation of plausible alternative strategies constitutes the subject of a separate study, it is worth noting a few possibilities. In addition to testing how long cutting cycles ought to be to achieve STY under the current federally mandated guidelines (i.e., for seed trees and MDF), different aspects of the intensive management treatment could be tested alone and at different intensities to determine their potential benefits. For example, the liana cutting treatment could be applied every 15 years instead of at each harvest entry, or it could be applied to more trees, or both. Similar experiments could be simulated for the poison-girdling and scarification treatments. Finally, it would be worthwhile to simulate management regimes that alter the MDF, as was recently done by Arets (2005) for Guyanese forests.

Management Treatment Impacts on Forest Structure and Composition

Total tree density and basal area

In the absence of logging or additional silviculture, total tree density slightly decreased and total basal area slightly increased over 60 years, which leads to the inference that the basal area increase is mainly attributable to growth of existing trees. The fact that tree density did not substantially increase is surprising at first glance considering that the tree density (> 10 cm dbh) in La Chonta is at the lower end of the range (371–768 trees / ha) found in other neotropical forests by Dewalt and Chave (2004). On the other hand, the fact that 73% of trees (> 10 cm dbh) are liana infested (Alvira et al. 2004) probably contributes to relatively high annual mortality rates (about 3% per year) compared to the 2% annual mortality rates commonly reported for tropical forests (Phillips et al. 2004a). In addition, this result could be explained by La Chonta's relatively open structure and the fact that up to 30% of the area is in gap or building phase (Chapter 1). Although we would expect succession to proceed in these areas over the long term, it is conceivable that, over the short- or medium-term, the high liana densities along with dense patches of giant herbs (e.g., *Heliconia* spp.) and understory trees (e.g., chocolatlillo) that have probably slowed succession to date, would continue to do so in the absence of any management interventions. One can imagine that as succession eventually proceeds in existing patches dominated by herbs, lianas, and treelets to trees capable of reaching the canopy, new open patches form. The observed basal area increase occurred mostly in the long-lived pioneers, which in the field appear robust and would probably continue growing over the 60-year period simulated, and among the shade-tolerant trees that dominate the sub-canopy.

The simulated harvest treatments did not appreciably alter the projected changes in total tree density and basal area observed in the control treatment. Other studies have reported more substantial changes in tree density and basal area following logging (Silva et al. 1995, Pinard and Putz 1996, Bertault and Sist 1997, Sist 2000, Arets 2005). The relatively modest impact reported here is explained by the relatively low harvest intensities (even in the ‘intensive’ management treatment in La Chonta), which only reduced basal area by 11–15% and obtained timber volumes of 11–15 m³/ha. By tropical standards these harvest treatments were of very low intensity (Putz et al. 2001).

Impacts at the species group level

In the absence of logging, the model projections indicate that the shade-tolerant canopy species would become increasingly dominant in the stand at the expense of the light-demanding canopy species, which is consistent with successional theory and field observations elsewhere (e.g., Horn 1974, Connell and Slayter 1977, Finegan 1996, Peña-Claros 2003). The long-lived pioneers, which are also light-demanding, remained dominant in the stand over the 60 year simulation period. This result is not too surprising considering the relatively short simulation time and the observation that the large individuals of this species group did not appear senescent in the field. The reduction in basal area of the light-demanding canopy species is consistent with expectations considering their relatively slow growth rates relative to the pioneer species groups and poor recruitment compared to all the other species groups.

The harvest treatment effects were barely detectable because of their low relative intensity, and hence the overall patterns were similar to those observed in the control treatment. Nevertheless, the harvest of shade-tolerant species and the silviculture applied in the intensive management treatment slowed the increase in relative dominance

over time of the shade-tolerant species projected for the other treatments. These relatively minor changes contrast with other simulation studies of logging impacts on tropical forest structure and composition, which typically find a shift in species composition (Favrichon 1998, Kammesheidt et al. 2001) marked by a strong initial response from colonizing, and other, pioneer species (Huth and Ditzer 2001, Phillips et al. 2004b, Arets 2005), and/or a significant reduction in the percentage of commercial species in the residual stand especially if logging impacts are severe (Liu and Ashton 1999).

The intensive management treatment clearly promoted the growth and recruitment of some of the targeted commercial species, but was apparently less successful with others. For example, long-lived pioneers recruited and grew better under intensive management than under the normal harvest treatment. In contrast, although the light demanding species performed better under the intensive management treatment than under the normal harvest treatment, they obviously require more intensive silviculture to sustain their present relative abundance and basal area in La Chonta. The poor recruitment and slow growth rates of most species in this group have already been documented in this region (Mostacedo and Fredericksen 1999).

Reliability of the Model's Projections

Lacking long-term data to validate the model, I only tested the calibrated data set against independent non-calibration data from the same site. Although less ideal than validation with long-term data, this approach nevertheless provided some basis by which to judge the reliability of the model's projections for La Chonta. The similarity between the calibrated and test datasets in terms of growth rates, species group composition, total

tree density, and extent of liana infestation provided some basis for concluding that the model's projections would be generally applicable to the site.

The higher recruitment rate for colonizing pioneers in the calibration dataset than in the test dataset caused me to question the reliability of initial projections based on the parameterized recruitment functions. In particular, the doubling of the density and basal area of the colonizing pioneers in initial simulations under the no logging treatment was a counterintuitive result that was inconsistent with field observations in the control plots. The results with the adjusted recruitment model were more sensible; the density and basal area of colonizing pioneers did not change appreciably in the control treatment.

Although no forest like La Chonta in Bolivia has yet undergone a second harvest under the current management guidelines, the projections obtained here are consistent with foresters' expectations and with the results of Dauber et al. (2005). In particular, the recoverable volumes estimated in this study for the 2nd cut were quite similar to the estimates in Dauber et al. (2005) for forests in the same region treated under the normal harvest regime especially. The intensive management treatment of this study is more conservative than the optimal scenario of Dauber et al. (2005), and logically resulted in lower recoverable volumes.

Although this model provides a first approximation of the likely outcomes of the silvicultural experiment, it could be improved if two principal weaknesses are addressed as more data become available. The first weakness concerns the time span of the data: two years of census information is barely adequate to calibrate empirical models of growth, mortality and recruitment. The paucity of data, especially for large trees, made the parameter estimates for these models quite uncertain. Moreover, the short time span

of the data means that variation in growth, mortality, and recruitment rates due to climate change were not captured.

The model's second weakness is its dependence on simplifying assumptions rather than data for some key ecological processes. For example, this model assumed that trees of all species groups would respond to competition in the same way. Likewise, despite evidence to the contrary (e.g., Dalling et al. 2002), this model assumed that species groups were neither dispersal nor recruitment limited; that is, all species groups could recruit anywhere in the simulated stand. Finally, although lianas strongly affect growth, mortality, and recruitment rates of tropical trees (e.g., Schnitzer et al. 2000, Gerwing 2001, Alvira et al. 2004, Grauel and Putz 2004), this model only incorporates the limited information available on lianas and their effects in La Chonta. This dependence on assumptions resulted from lack of data as well as a need to make the model tractable. As more data become available, it will be possible to replace assumptions with calibrated parameters.

Sensitivity of the Model to Parameters Based on Little or No Data

Although a full sensitivity analysis of the model was beyond the scope of this study and, in fact, would constitute its own study, it was important to determine the extent to which parameters estimated based on little or no data (i.e., liana infestation rate, damage related mortality, large tree mortality, and silvicultural effects on recruitment) would influence the projections. Because relatively large changes in the values of these parameters resulted in relatively small changes in the tested response variables (i.e., tree density, basal area, and the proportion of liana-infested trees), I conclude that the model is not particularly sensitive to these parameters.

Nevertheless, it is important to note that untested response variables could be more sensitive to these parameters. In particular, considering the large effects of damage related mortality observed in other simulation models (e.g., Liu and Ashton 1999), and the uncertainty concerning the growth and mortality of large trees (Clark and Clark 1999), the accuracy of the model might be improved with additional data to properly estimate these parameters.

Conclusions

SYMFOR was a useful tool to assess the likely outcome of the silvicultural experiment established in La Chonta, but would obviously be improved with additional field data to parameterize key ecological processes that are central to the model rather than relying on simplifying assumptions. A principal objective of the experiment was to determine whether intensive management would improve the prospects for achieving sustained yields of the currently commercial timber species. According to the projections in this study, the intensive management treatment comes closer to achieving STY than the normal harvest treatment, but still falls far short. Apparently, to achieve STY in these forests, foresters and managers will have to

- Implement management regimes even more intensive than the treatment applied in La Chonta;
- Accept longer cutting cycles; or,
- Find markets for and harvest a greater variety of species.

Further studies will be needed to determine what combination of these management strategies will best achieve sustained timber yields let alone other goods and services.

Table 2-1. Species groups obtained in the cluster and discriminant analyses.

SG	Species group name	N spp.	N trees	Mean growth (mm/yr)	Max. height (m)	Representative species
1	Understory shade-tolerant	45	3,190	1.58 ± 0.04	19	<u>Hirtella triandra</u> , <u>Stylogyne ambigua</u> , <u>Licaria triandra</u>
2	Long-lived pioneers	34	3,875	6.25 ± 0.12	39	<u>Hura crepitans</u> , <u>Gallesia integrifolia</u> , <u>Ficus boliviana</u>
3	Slow-growing shade-tolerant canopy	10	7,518	2.44 ± 0.03	35	<u>Pseudolmedia laevis</u> , <u>Ocotea</u> sp., <u>Myrciaria</u> sp.
4	Dry forest	8	1,047	2.55 ± 0.11	31	<u>Aspidosperma rigidum</u> , <u>Caesalpina pluviosa</u> , <u>Aspidosperma cylindrocarpon</u> , <u>Terminalia oblonga</u> , <u>Pouteria nemorosa</u> , <u>Cariniana iarensis</u>
5	Light-demanding canopy	20	3,611	2.92 ± 0.07	36	<u>Pourouma cecropifolia</u> , <u>Sapium glandulosum</u> , <u>Schizolobium parahyba</u>
6	Intermediate-lived pioneers	25	1,072	6.32 ± 0.27	33	<u>Urera</u> sp., <u>Jacaratia spinosa</u> , <u>Heliocarpus americanus</u>
7	Colonizing pioneers	8	1,534	6.99 ± 0.26	23	<u>Ampelocera ruizii</u> , <u>Ocotea</u> sp., <u>Dendropanax arboreus</u>
8	Fast-growing shade-tolerant canopy	3	2,822	6.17 ± 0.11	32	

Notes: SG = species group number; N spp. = number of species in the corresponding SG; N trees = number of valid records for height.

Table 2-2. Estimated parameter values for diameter increment in La Chonta obtained by non-linear regression with growth modeled as a function of dbh and liana class for each species group.

SG	N	Estimated parameters for dbh increment						Variance explained: R ² (%)		Parameters for large tree growth rate		
		<i>p</i> ₀	<i>p</i> ₁	<i>p</i> ₂	<i>p</i> ₃	<i>p</i> ₄	<i>p</i> ₅	Full model	Dbh means	<i>p</i> ₆	<i>p</i> ₇	<i>D</i> ₉₅
1	2,608	-0.3774	0.0000	0.0164	0.0255	-0.0104	0.0310	4.8	57.2	-0.0966	0.2497	23.6
2	2,687	-0.4693	0.0013	0.0492	0.0334	-0.0836	0.2496	5.1	50.9	-0.2678	0.5879	98.4
3	6,499	-0.3334	0.0076	0.1235	0.1771	-0.0342	0.0462	7.4	86.1	-0.0768	0.3668	38.9
4	817	-0.4845	0.0034	0.0308	0.0510	-0.0249	0.0564	7.6	36.2	-0.1537	0.3474	47.9
5	2,632	-0.4932	0.0000	0.0285	0.0281	-0.0297	0.0758	5.1	26.3	-0.1520	0.3113	79.5
6	8,96	-0.5187	0.0000	0.0714	0.0257	-0.1027	-0.0454	9.4	65.6	-0.5168	0.9521	44.3
7	1,108	-0.5767	0.0011	0.1361	0.0623	-0.1569	0.1832	11.3	63.0	-0.2077	0.4366	45.2
8	2,223	-0.3630	0.0110	0.0799	0.0547	-0.0431	0.0115	7.4	61.0	-0.2113	0.7870	44.2

Notes: See Table 2-1 for species group (SG) names. N = number of trees with valid growth records. Parameters *p*₀-*p*₅ were estimated using Eq. 2-3. The first R² value indicates the percentage of variation in growth rates due to all sources (dbh, competition, and liana class) included in the regressions explained by the model (*P* < 0.001). The second R² value indicates the percentage of observed variation in the growth rates for each dbh class (see Eq. 2-4 and Figure 2-2). The parameters *p*₆ and *p*₇ are used in Eq. 2-5 and give the growth rate for large trees (dbh ≥ *D*₉₅).

Table 2-3. Estimated ingrowth parameters and associated R^2 values obtained from weighted non-linear regression using Eq. 2-6.

SG	N recruits	i_1	i_2	R^2	Max. growth (cm/yr)	T_i
1	87	0.0725	6.1633	23.4	0.23	62
2	26	0.0014	-2.6386	57.2	1.18	14
3	67	0.0827	4.2986	91.3	0.56	26
4	7	0.0009	-3.0359	52.2	0.44	33
5	23	0.0051	-1.2238	67.7	0.49	30
6	17	0.0023	-1.5237	12.2	1.20	14
7	87	0.0254	-0.1107	0.9	1.98	9
8	50	0.0697	2.5812	41.9	0.87	18

Notes: N recruits = ingrowth into the 10 cm dbh class between census 0 and census 2. Max. growth = maximum growth rates for juvenile trees (dbh from 10–20 cm). Values for T_i were calculated assuming that the time from seedling establishment to 1 cm is 50% of the time required for trees to grow from 1 to 10 cm and that growth rates from 1 to 10 cm equal growth rates from 10 to 20 cm.

Table 2-4. Estimated mortality parameters obtained from logistic regression using Eq. 2-7.

SG	Liana class (L)	Parameter	Estimate	Std. error	Z-value	P
All	Both	Intercept	-2.7499	0.2643	-10.40	<0.0001
1	Both	m_1	0.0000	—	—	—
2	Both	m_1	0.0429	0.2378	0.16	0.87
3	Both	m_1	-0.5894	0.2162	-2.73	0.01
4	Both	m_1	-0.0577	0.4562	-0.13	0.90
5	Both	m_1	-0.1605	0.2645	-0.61	0.54
6	Both	m_1	0.5798	0.2821	2.06	0.04
7	Both	m_1	0.9797	0.2542	3.85	0.00
8	Both	m_1	0.1524	0.2530	0.60	0.55
All	Both	m_2	-0.0245	0.0087	-2.83	0.00
All	0	m_3	0.0000	—	—	—
All	1	m_3	-0.0066	0.2738	-0.02	0.98
All	0	m_4	0.0000	—	—	—
All	1	m_4	0.0207	0.0092	2.24	0.02

Table 2-5. Parameter values for the mortality constant of large, liana-free and liana-infested trees of each species group in La Chonta.

SG	a_1	a_2	D_{95} for L_0	D_{95} for L_1
1	0.0086	0.0209	18.2	21.8
2	0.0176	0.0063	69.9	91.5
3	0.0082	0.0075	36.6	37.9
4	0.0134	0.0116	40.3	51.2
5	0.0147	0.0066	59.7	68.5
6	0.0244	0.0237	36.5	38.1
7	0.0316	0.0371	33.7	41.1
8	0.0178	0.0134	42.9	45.9

Notes: The mortality constant is m_{95} from Eq. 2-10 and is used in the function for supplemental mortality of large trees ($\text{dbh} > D_{95}$) in Eq. 2-9. D_{95} = the 95th percentile of the dbh distribution for liana-free (L_0) and liana-infested (L_1) trees.

Table 2-6. Liana infestation probabilities used for assigning a liana class to new recruits.

SG	Neighborhood liana infestation class							
	0–0.25		0.25–0.5		0.5–0.75		0.75–1.0	
	N	P_L	N	P_L	N	P_L	N	P_L
1	9	0.13	209	0.36	566	0.60	237	0.81
2	1	0.17	13	0.26	39	0.36	26	0.57
3	9	0.12	101	0.32	310	0.57	133	0.73
4	0	0.00	15	0.41	45	0.62	15	0.79
5	2	0.25	36	0.37	92	0.57	45	0.65
6	0	0.00	5	0.12	41	0.45	19	0.70
7	1	0.02	8	0.12	20	0.31	9	0.56
8	2	0.09	28	0.21	107	0.53	48	0.74

Notes: The probabilities (P_L) equal the proportion of juvenile trees ($\text{dbh} < 15$) with lianas in each corresponding neighborhood liana infestation class. N= number of liana-infested juvenile trees of each species group (SG) in the corresponding neighborhood liana infestation class.

Table 2-7. Assigned probability of simulated gaps becoming liana infested depending on the liana class (L) of the falling tree and the proportion of neighbors with lianas.

L of falling tree	Percent neighbors with lianas	Probability of liana tangle
0	<50	0.0
0	>50	0.1
1	<50	0.2
1	>50	0.4

Table 2-8. Dbh and total tree height allometric relationship parameter estimates and associated R^2 values for each species group.

SG	n	R^2	h_{\max}	h_1	h_2
1	240	82.5	87.6755	0.0279	0.5751
2	237	89.0	84.0418	0.0353	0.5860
3	100	92.3	30.6498	0.0576	0.9003
4	80	90.6	40.8618	0.0460	0.7609
5	218	90.9	54.9887	0.0357	0.7644
6	102	91.4	82.6537	0.0312	0.6455
7	113	81.8	29.3009	0.0602	0.8248
8	84	87.2	40.0021	0.0651	0.6972

Notes: Estimates obtained from non-linear regression (Eq. 2-11). The sample size (n) refers to the number of trees of each species group used to estimate the parameters.

Table 2-9. Parameter values used to calculate the crown-point (a) for each species group.

SG	N	a
1	0	0.35*
2	183	0.34
3	51	0.32
4	26	0.32
5	248	0.37
6	18	0.36
7	0	0.35*
8	6	0.32*

Notes: Crown-point is calculated using Eq. 2-13; it is used to calculate tree volume (Eq. 2-12). Values for species groups with asterisks are best guesses because data for these groups were unavailable or scanty. Source: IBIF (unpublished data).

Table 2-10. Mean wood density values for each species group and the number of species on which each mean is based.

SG	Mean wood density	Number of species
1	0.62	13
2	0.48	14
3	0.64	5
4	0.77	6
5	0.60	8
6	0.43	9
7	0.29	5
8	0.56	3

Notes: Wood density is used in the functions for supplemental mortality of large trees (Eq. 2-9), biomass (Eq. 2-14) and necromass (Eq. 2-15). Source: L. Poorter (unpublished data) and Chudnoff (1984).

Table 2-11. Utility group assignment for commercial and potentially commercial species in La Chonta.

<u>Species</u>	<u>Species group</u>	<u>Utility group</u>
<u>Centrolobium microchaete</u>	2	1
<u>Cordia alliodora</u>	2	1
<u>Hymenaea courbaril</u>	2	1
<u>Spondias mombin</u>	2	1
<u>Ficus boliviana</u>	2	2
<u>Hura crepitans</u>	2	2
<u>Swietenia macrophylla</u>	2	2
<u>Gallesia integrifolia</u>	2	3
<u>Batocarpus amazonicus</u>	3	3
<u>Pseudolmedia laevis</u>	3	3
<u>Aspidosperma cylindrocarpon</u>	4	1
<u>Caesalpinia pluviosa</u>	4	1
<u>Cariniana domestica</u>	5	1
<u>Cariniana estrellensis</u>	5	1
<u>Cariniana ianeirensis</u>	5	1
<u>Pouteria nemorosa</u>	5	1
<u>Tabebuia serratifolia</u>	5	1
<u>Terminalia oblonga</u>	5	1
<u>Ceiba samauma</u>	5	3
<u>Sweetia fruticosa</u>	5	3
<u>Schizolobium parahyba</u>	6	1
<u>Ampelocera ruizii</u>	8	3

Notes: Commercial species = utility groups 1 and 2; potentially commercial species = utility group 3.

Table 2-12. Proportional representation of each utility group in each species group in La Chonta.

Species group	Utility group	N	Percent of species group
1	4	3,451	100
2	1	485	12
2	2	1,607	39
2	3	410	10
2	4	1,597	39
3	3	6,270	79
3	4	1,624	21
4	1	473	42
4	4	640	58
5	1	2,690	71
5	3	196	5
5	4	879	23
6	1	148	13
6	4	1,020	87
7	4	1,751	100
8	3	1,452	48
8	4	1,585	52

Table 2-13. Scarification factor (E_s) estimates for adjusting the probability of recruitment of trees of each species group in scarified felling gaps.

SG	E_s
1	1.0*
2	2.2
3	0.9
4	1.0*
5	1.2
6	2.2
7	2.0
8	0.8*

*Values are best guesses because no or insufficient data existed for these species groups.

Table 2-14. Parameters and values tested in sensitivity analysis.

Parameter	Function	Baseline	Values tested
m_5	Supplemental mortality of large trees (Eq. 2-9)	Colonizing pioneers = 0.2; other species groups = 0.05	All species groups except colonizing pioneers: +/- 50%; all species groups: no supplemental mortality (i.e., $m_5 = m_{05}$); 0.1 +/- 50%; +100%; 0.015
L_c	Liana infestation rate (see Appendix B)	0.0475	+/- 50%; +100%; 0.015
P_f	Probability a tree dies falling (vs. standing)	0.1	+/- 50%
P_d	Probability a falling dead tree will kill a neighbor	0.3	+/- 50%
D_f	Minimum dbh below which a tree will only die standing	20	+/- 50%
T_i	Years required for a tree to recruit in a forest area (grid square) cleared of all vegetation (e.g., in a skid trail or scarified area)	See Table 2-3	+/- 50%; all species groups = 20 yrs
E_s	Increases or decreases the probability of recruitment for each species group in scarified forest patches	See Table 2-14	+/- 50%; 1 (i.e., no effect) for all species groups

Table 2-15. Per capita recruitment for each species group in the calibration and test datasets from La Chonta.

SG	Dataset	
	Calibration	Test
1	6.8	9.4
2	2.7	5.6
3	3.2	4.4
4	2.5	2.6
5	3.4	4.2
6	3.5	6.6
7	13.4	12.5
8	4.4	9.5

Note: Values are the ratio of recruits to adults for each species group in each dataset.

Table 2-16. Mean tree density and basal area by species group and as a proportion (%) of the totals in the calibration and test datasets.

SG	Mean tree density (stems/ha)				Mean basal area (m ² /ha)			
	Calibration		Test		Calibration		Test	
	Stems/ha	%	Stems/ha	%	Stems/ha	%	Stems/ha	%
1	80.3 ± 3.7	23.0	72.9 ± 4.2	19.1	1.4 ± 0.1	6.6	1.3 ± 0.1	7.1
2	34.3 ± 2.2	9.8	27.0 ± 3.2	7.1	6.3 ± 0.5	30.2	4.2 ± 0.5	22.0
3	110.2 ± 10.0	31.5	146.1 ± 10.8	38.3	4.5 ± 0.6	21.5	5.3 ± 0.6	28.1
4	12.7 ± 1.4	3.6	10.1 ± 1.6	2.6	0.7 ± 0.1	3.3	0.5 ± 0.1	2.4
5	39.6 ± 2.0	11.3	35.9 ± 2.3	9.4	4.5 ± 0.4	21.6	3.5 ± 0.3	18.2
6	14.3 ± 1.8	4.4	22.6 ± 4.1	5.9	0.7 ± 0.1	3.4	1.2 ± 0.2	6.5
7	20.5 ± 3.3	5.9	19.1 ± 2.0	5.0	1.0 ± 0.1	4.7	0.9 ± 0.1	4.8
8	38.0 ± 2.0	10.9	47.4 ± 4.3	12.4	1.8 ± 0.1	8.7	2.1 ± 0.1	10.9

Notes: Errors are standard error of the mean based on variation across 1 ha plots (n=16 for the test dataset and 32 for the calibration dataset).

Table 2-17. Sensitivity of tree density and basal area of each species group to changes in supplemental mortality of large trees.

SG	No supplemental mortality ($m_5 = m_{95}$)				$m_5 = 0.1$			
	Tree density		Basal area		Tree density		Basal area	
	%	S	%	S	%	S	%	S
1	0.05	0.10	0.02	0.04	-0.02	-0.04	-0.06	-0.12
2	-0.08	-0.15	-0.06	-0.11	0.00	0.00	-0.05	-0.11
3	0.07	0.15	0.08	0.15	0.00	-0.01	-0.04	-0.08
4	0.00	0.01	0.19	0.39	0.00	0.00	-0.02	-0.04
5	-0.01	-0.02	0.07	0.14	-0.01	-0.01	-0.08	-0.16
6	-0.03	-0.07	0.20	0.40	-0.03	-0.05	-0.23	-0.47
7	0.12	0.12	0.40	0.40	0.04	0.09	0.11	0.22
8	-0.02	-0.03	0.26	0.52	-0.03	-0.06	-0.18	-0.36

Notes: Supplemental mortality of large trees is determined by the parameter m_5 in Eq. 2-9. Values below % refer to percent changes in tree density and basal area observed with $m_5 = m_{95}$ or $m_5 = 0.1$ relative to the baseline (see Table 1-15). Values below S refer to the sensitivity (from Eq. 2-16) of tree density and basal area to changes in m_5 .

Table 2-18. Simulated harvest results from the normal harvest treatment by species and utility group at years 0, 30, and 60.

SG	Utilgrp	N plots			N trees			Volume		
		Year-0	Year-30	Year-60	Year-0	Year-30	Year-60	Year-0	Year-30	Year-60
2	1	8	9	13	0.20 ± 0.07	0.13 ± 0.05	0.24 ± 0.05	0.48 ± 0.19	0.25 ± 0.09	0.43 ± 0.11
4	1	5	1	1	0.09 ± 0.04	0.03 ± 0.03	0.04 ± 0.04	0.18 ± 0.08	0.03 ± 0.03	0.06 ± 0.06
5	1	14	15	15	1.52 ± 0.33	0.53 ± 0.06	0.20 ± 0.04	5.48 ± 1.09	1.56 ± 0.21	0.52 ± 0.11
6	1	0	2	3	0.00 ± 0.00	0.02 ± 0.01	0.04 ± 0.02	0.00 ± 0.00	0.04 ± 0.03	0.08 ± 0.05
2	2	13	11	8	0.55 ± 0.12	0.28 ± 0.06	0.09 ± 0.03	4.19 ± 1.06	1.48 ± 0.39	0.35 ± 0.12

Notes: N plots = the number of test plots in which trees of the corresponding species and utility groups were harvested; N trees = the mean number of trees harvested (±standard error) across the 15 test plots; and Volume = mean volume (±standard error) harvested among the test plots. See Table 2-1 for species group (SG), and Tables 2-12 and 2-13 for utility group (UtilGrp) definitions.

Table 2-19. Simulated harvest results from the intensive management treatment by species and utility group at years 0, 30, and 60.

SG	Utilgrp	N plots			N trees			Volume		
		Year-0	Year-30	Year-60	Year-0	Year-30	Year-60	Year-0	Year-30	Year-60
2	1	8	12	13	0.24 ± 0.10	0.35 ± 0.10	0.33 ± 0.08	0.64 ± 0.31	0.70 ± 0.19	0.74 ± 0.19
4	1	5	4	5	0.08 ± 0.03	0.04 ± 0.03	0.05 ± 0.03	0.16 ± 0.08	0.11 ± 0.07	0.07 ± 0.04
5	1	14	15	15	1.80 ± 0.39	0.85 ± 0.12	0.36 ± 0.05	6.34 ± 1.23	2.36 ± 0.31	0.98 ± 0.12
6	1	0	5	5	0.00 ± 0.00	0.05 ± 0.02	0.04 ± 0.02	0.00 ± 0.00	0.12 ± 0.06	0.06 ± 0.03
2	2	13	13	14	0.87 ± 0.21	0.48 ± 0.08	0.37 ± 0.07	6.67 ± 1.62	2.55 ± 0.55	1.57 ± 0.42
2	3	6	7	10	0.21 ± 0.09	0.09 ± 0.04	0.09 ± 0.03	0.45 ± 0.19	0.26 ± 0.10	0.15 ± 0.05
3	3	7	11	13	0.17 ± 0.06	0.24 ± 0.08	0.32 ± 0.13	0.27 ± 0.10	0.33 ± 0.10	0.43 ± 0.18
5	3	1	3	6	0.00 ± 0.00	0.02 ± 0.01	0.04 ± 0.02	0.01 ± 0.01	0.04 ± 0.02	0.07 ± 0.03
8	3	7	11	14	0.11 ± 0.05	0.25 ± 0.06	0.39 ± 0.06	0.20 ± 0.08	0.40 ± 0.10	0.68 ± 0.11

Notes: Headings are the same as those in Table 2-18. Values below the dashed line are for potentially commercial species not harvested in the normal harvest treatment.

Table 2-20. Harvest volumes obtained (total and by commercial class) in years 0, 30, and 60 from simulations of the normal harvest and intensive management treatments in La Chonta.

Harvested species groups	Normal harvest volume (m ³ /ha)			Intensive management volume (m ³ /ha)		
	Year-0	Year-30	Year-60	Year-0	Year-30	Year-60
Commercial	10.33 ± 1.69	3.36 ± 0.42	1.44 ± 0.13	13.80 ± 3.24	5.84 ± 1.18	3.42 ± 0.80
Potentially commercial	—	—	—	0.93 ± 0.38	1.02 ± 0.32	1.33 ± 0.37
Total volume	10.33 ± 1.69	3.36 ± 0.42	1.44 ± 0.13	14.73 ± 2.40	6.86 ± 0.53	4.75 ± 0.37
Proportion (%) of initial volume recovered	—	32.5	13.9	—	46.6	32.3

Notes: Volumes are means based on 15 repetitions of 15 1-ha plots. The errors are standard errors of the mean arising from variation across plots.

Table 2-21. Relative contribution of silviculture and new species harvested to the increase in harvest volumes obtained with the simulated intensive management treatment compared to the normal harvest treatment.

Measure	Year-0	Year-30	Year-60
Proportion of total volume comprising commercial species (intensive management)	93.7	85.2	72.0
Relative increase in commercial volume due to silviculture	33.6	74.2	137.9
Relative increase in total volume due to intensive management	42.6	104.5	230.6
Proportion of increase in total volume due to silviculture	78.9	70.9	59.8
Proportion of increase in total volume due to new (potentially commercial) species	21.1	29.1	40.2

Note: Values are in %.

Table 2-22. Silvicultural liberation of future crop trees (FCTs) from lianas and neighboring competitors (by poison-girdling), and the proportion of felling gaps that were scarified in each cutting cycle in simulations of the intensive management treatment in La Chonta.

Harvest year	Number of FCTs liberated per ha via		Proportion of felling gaps scarified (%)
	Liana cutting	Poisoning neighbors	
0	26.0 ± 2.4	6.2 ± 0.6	37
30	23.8 ± 1.0	6.0 ± 0.4	41
60	23.5 ± 0.8	6.0 ± 0.0	40

Notes: Values are means based on 15 repetitions of 15 1-ha plots. Errors are standard errors of the mean based on variation across plots.

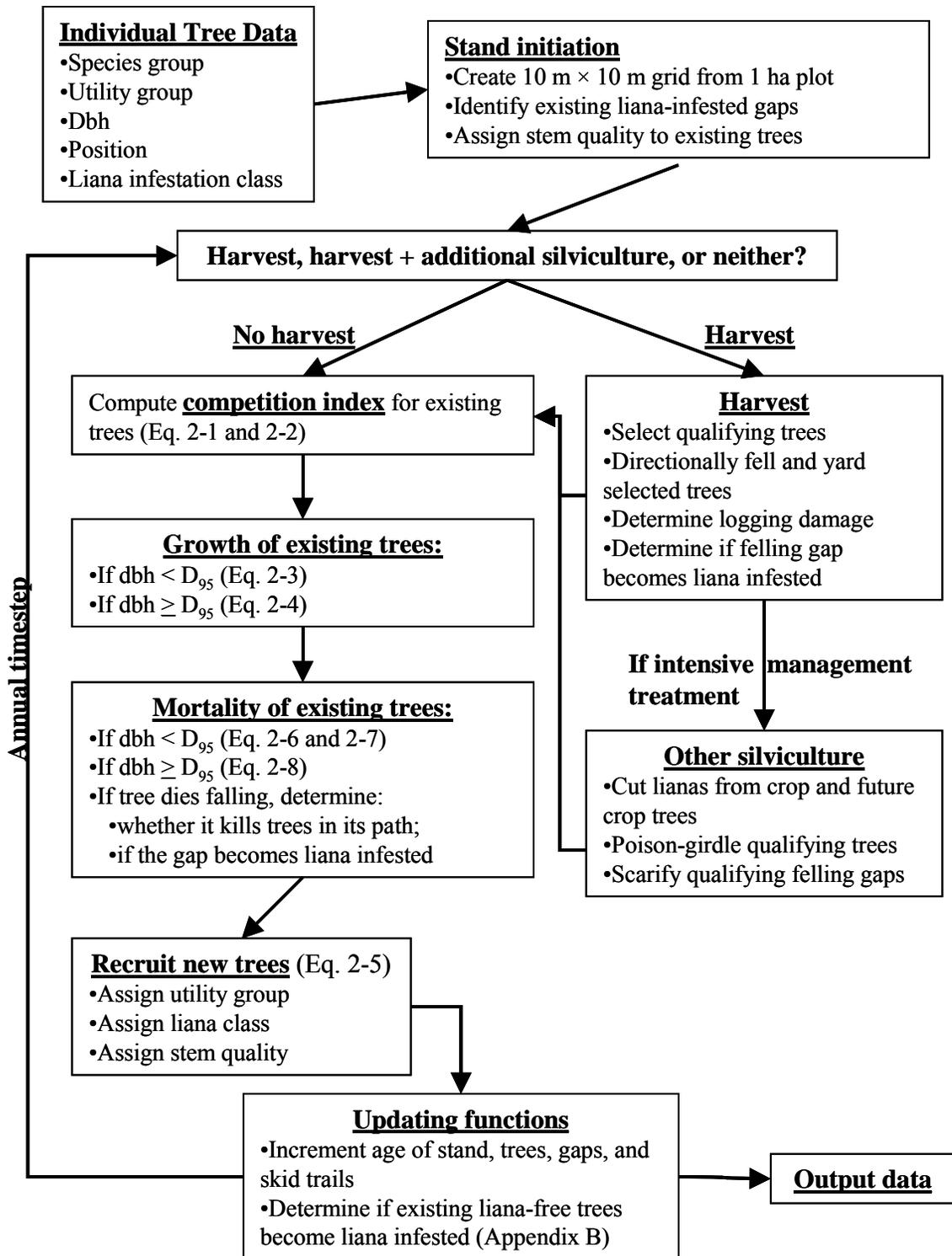


Figure 2-1. SYMFOR model overview and flow. SYMFOR uses the individual tree data from the 1 ha plots in the LTSRP in La Chonta as input to create a stand. Each of the subsequent steps (described in the boxes) occurs in the order indicated by the arrows in annual time steps. The user instructs SYMFOR which management model and how many years to simulate.

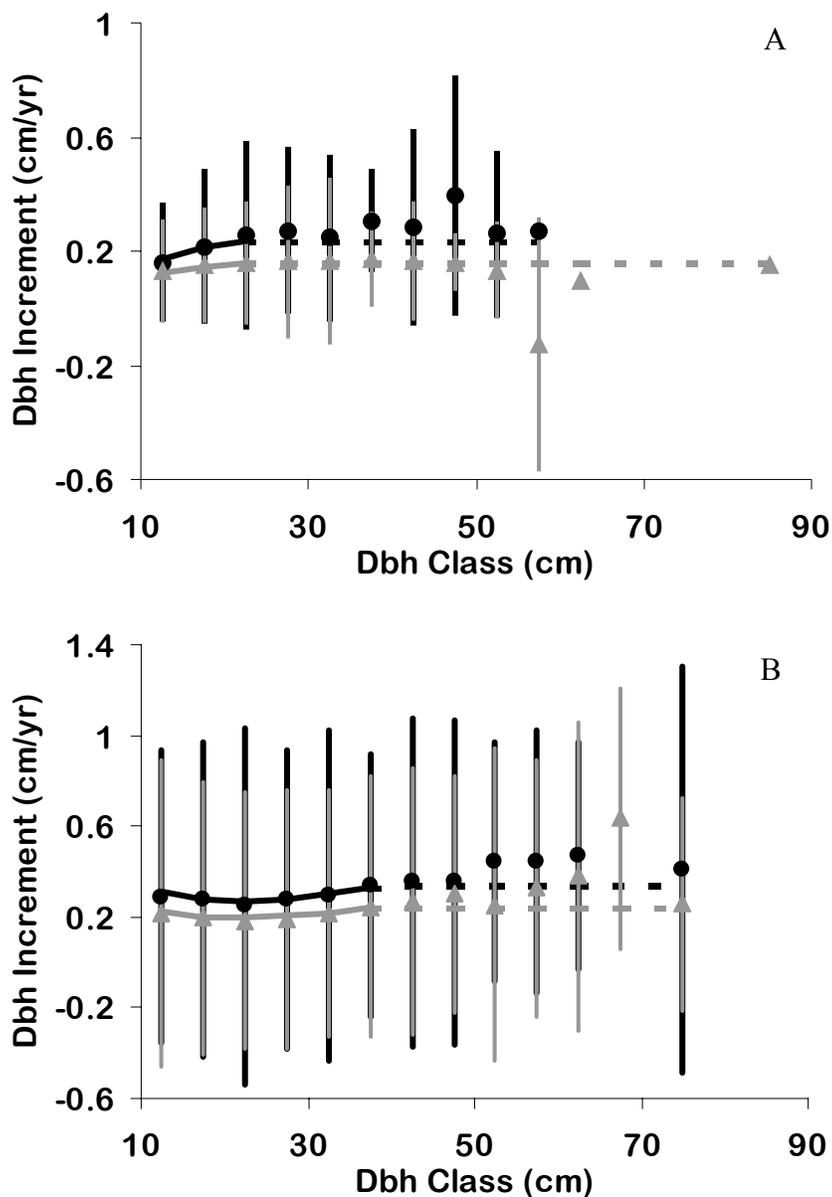


Figure 2-2. Dbh growth patterns for 8 species groups in La Chonta by liana class revealed by non-linear regression analysis. Black circles = mean growth rate (cm/yr) for each dbh class of liana-free trees. Gray triangles=mean growth rate for liana-infested trees. The bars indicate the standard deviation associated with each mean. The black and gray curves indicate the growth rate at average competition ($C=0$) predicted by the calibrated regression model for liana-free and liana-infested trees respectively. The flat, dashed part of the regression curves indicate the constant growth rate assumed for trees with $dbh > D_{95}$. A) Understory. B) Slow-growing shade-tolerant. C) Fast-growing shade-tolerant. D) Dry forest. E) Light-demanding. F) Long-lived pioneers. G) Intermediate-lived pioneers. H) Colonizing pioneers. I) Predicted growth rates for all species groups (liana-free trees). See Table 2-2 for sample sizes.

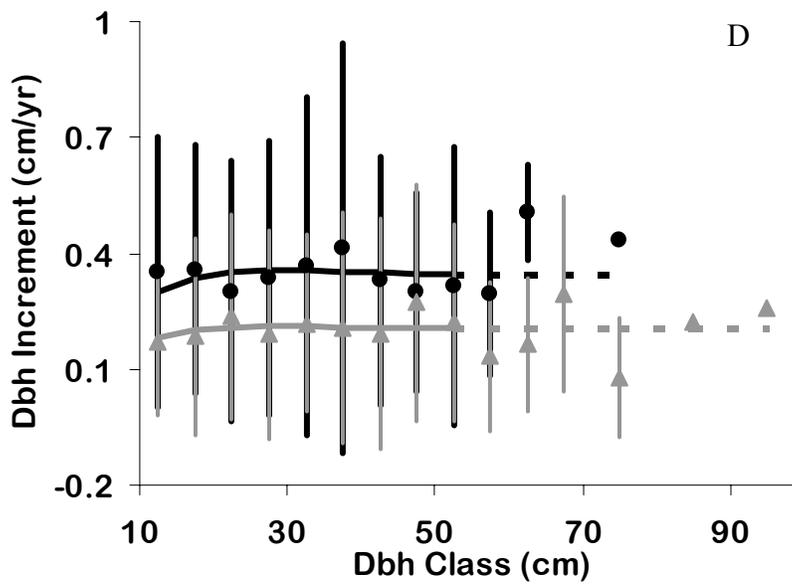
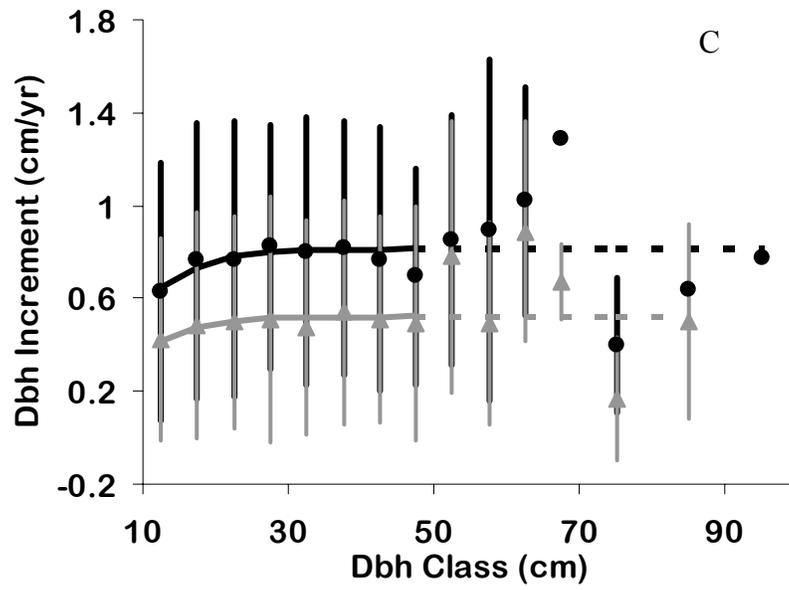


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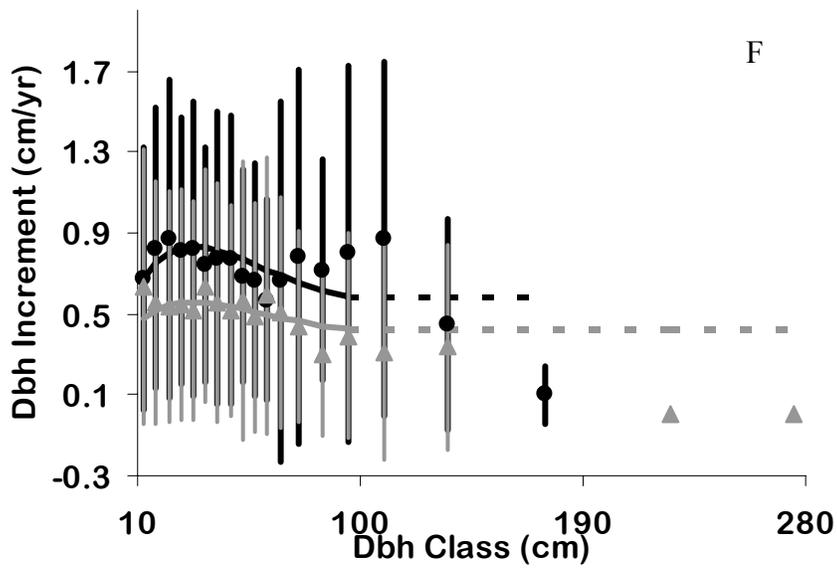
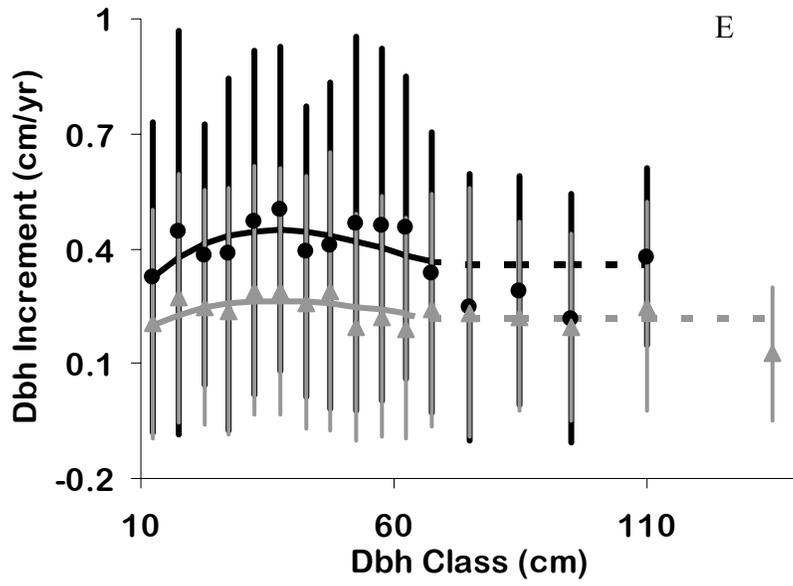


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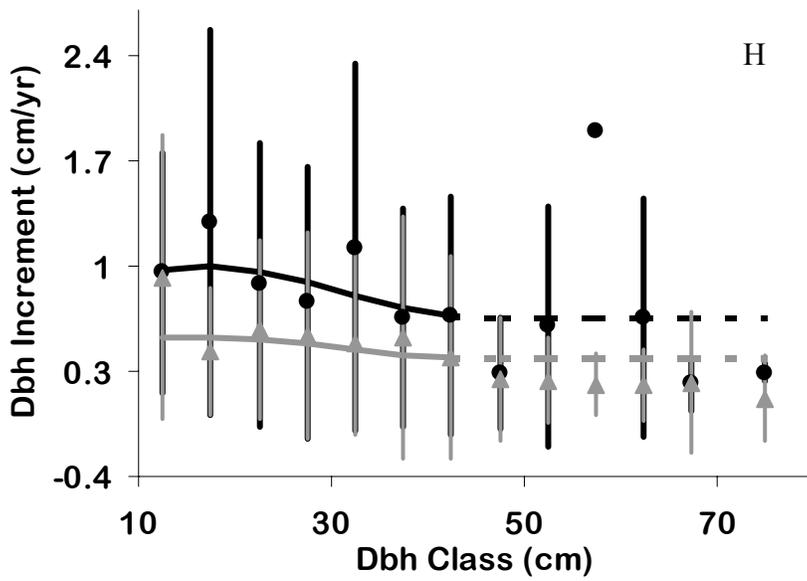
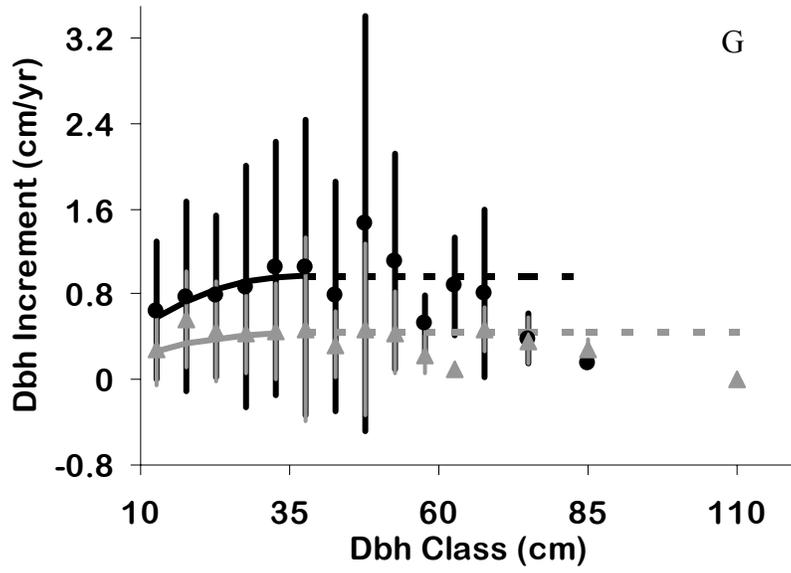


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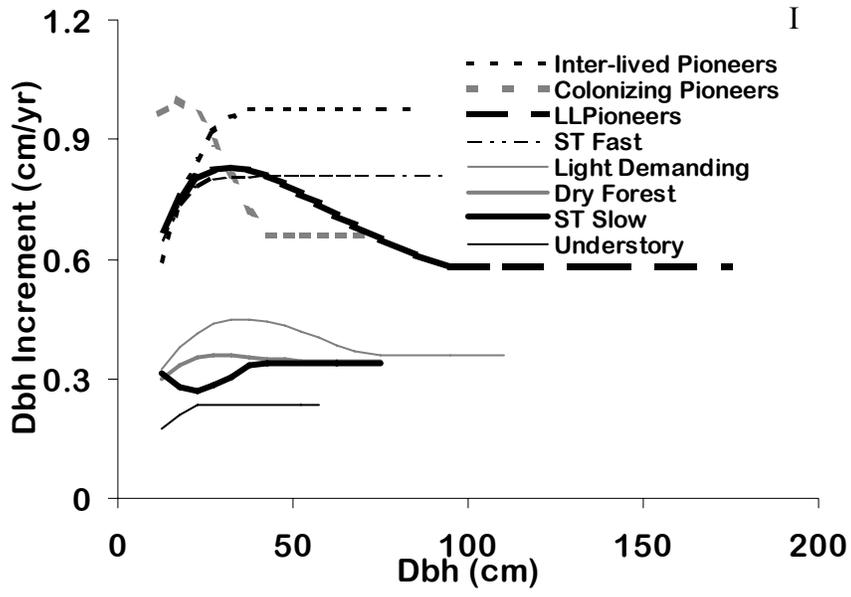


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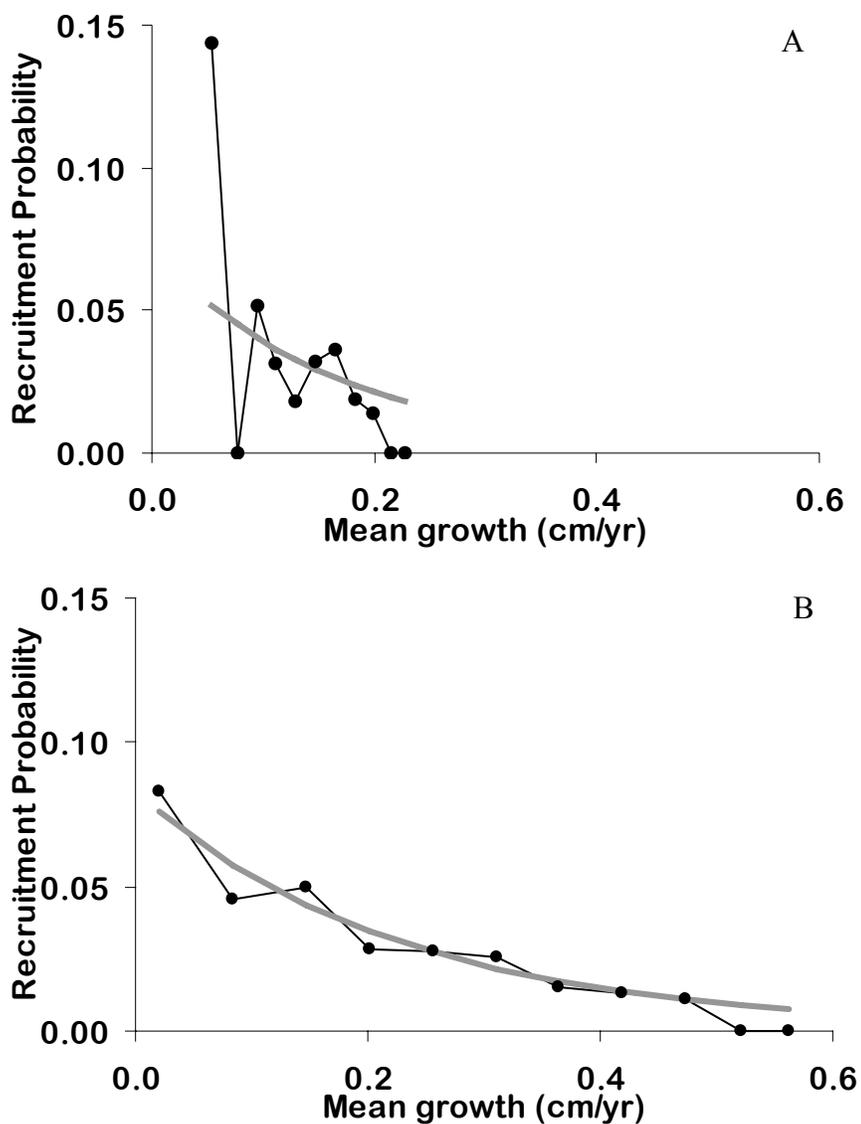


Figure 2-3. Probabilities of ingrowth calibrated by non-linear regression as a function of predicted growth rate for 10 cm recruits of the 8 species groups defined in La Chonta. Solid black circles represent the probability of recruitment from the data. The gray curves represent the recruitment probabilities based on the calibrated models for each species group. A) Understory. B) Slow-growing shade-tolerant. C) Fast-growing shade-tolerant. D) Dry forest. E) Light-demanding. F) Long-lived pioneers. G) Intermediate-lived pioneers. H) Colonizing pioneers. See Table 2-3 for total number of recruits for each species group and R^2 values. Note different scales on axes.

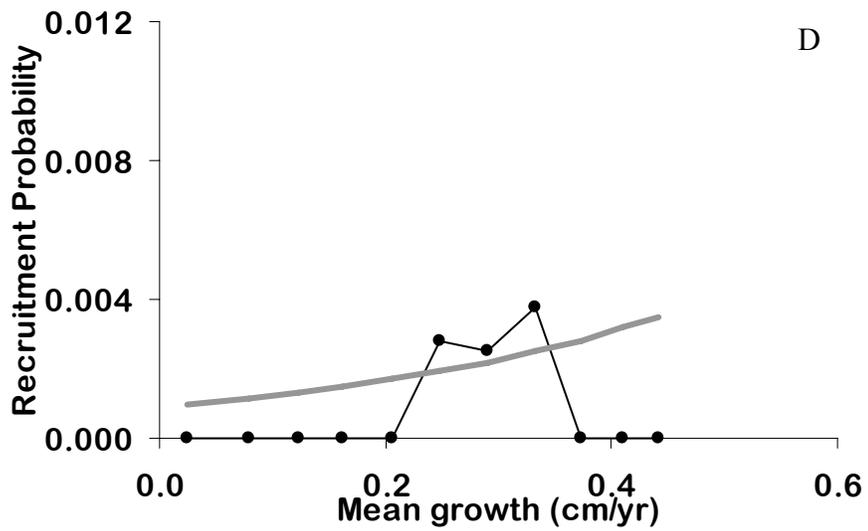
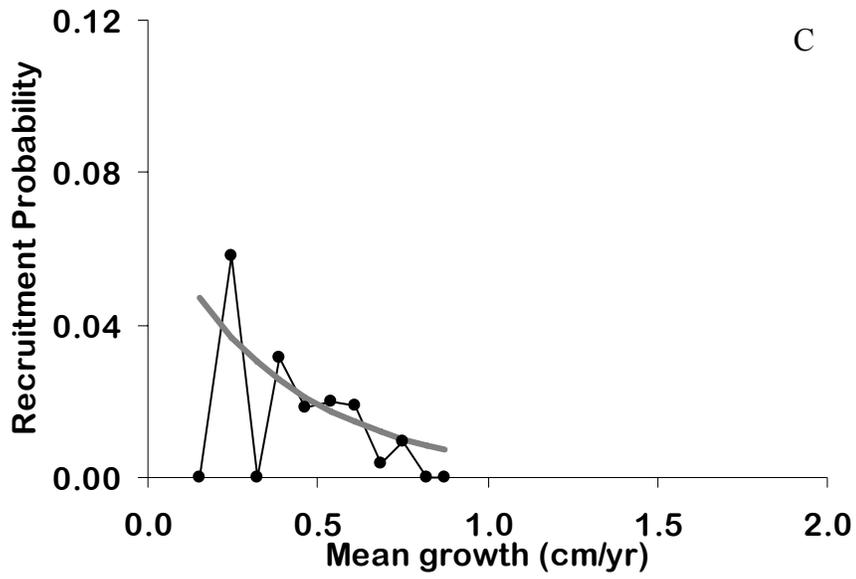


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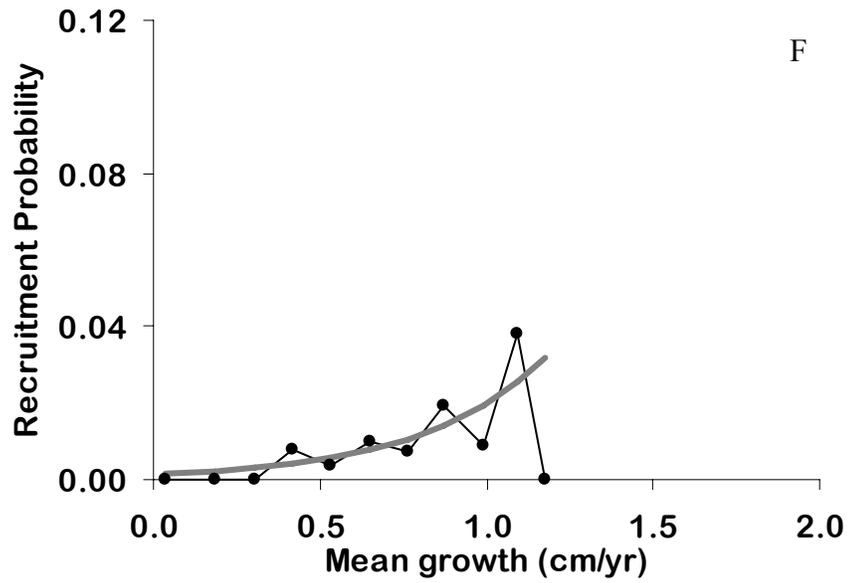
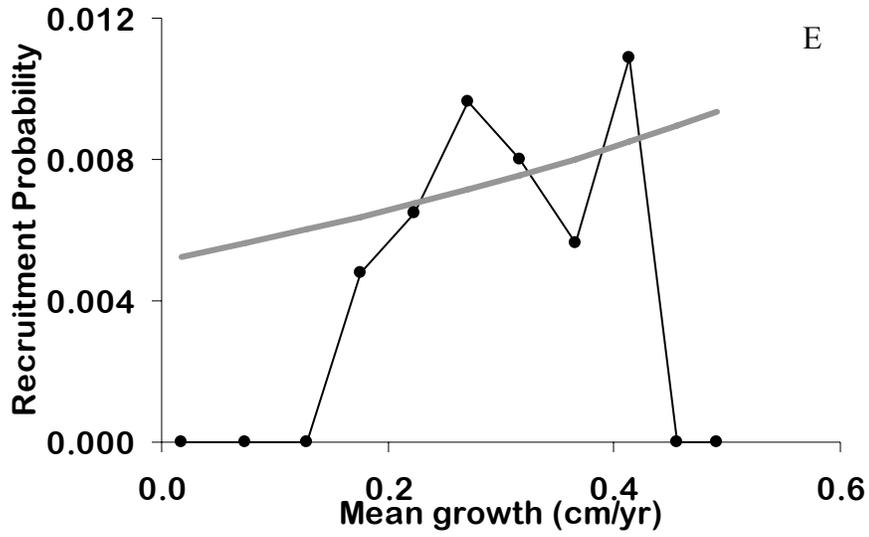


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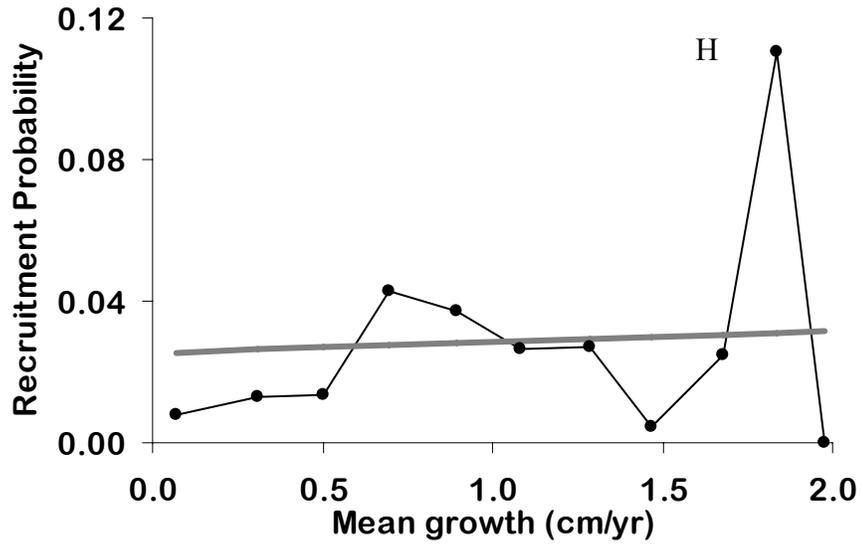
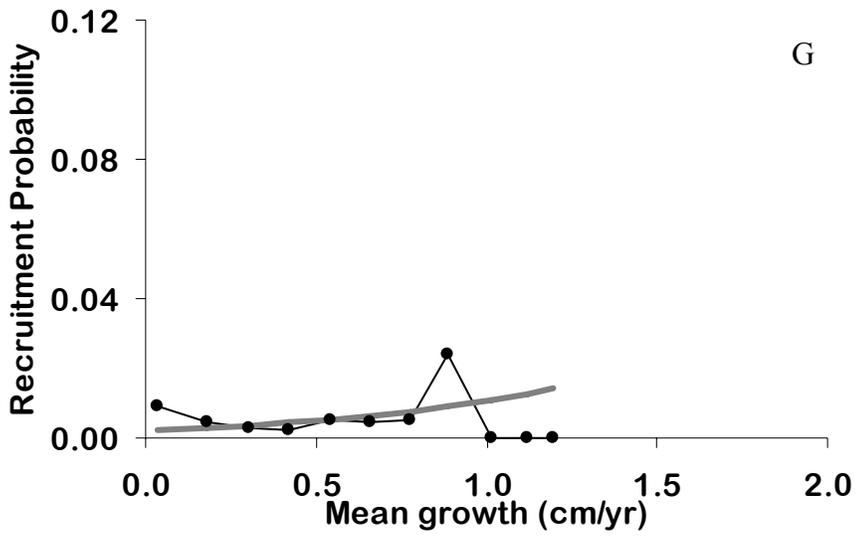


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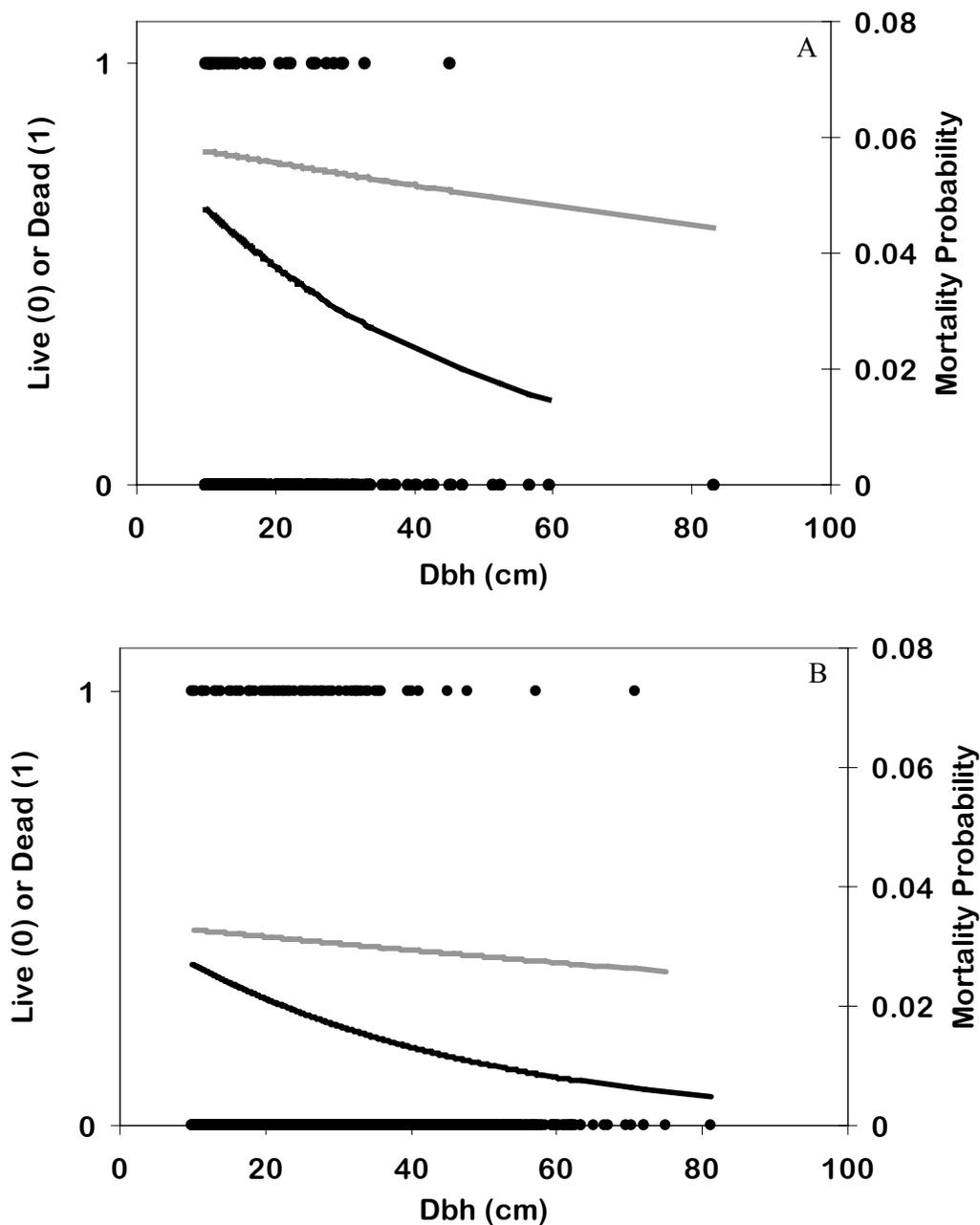


Figure 2-4. Probabilities of annual mortality calibrated by logistic regression as a function of dbh and liana class for the 8 species groups defined in La Chonta. Each of the solid black circles represents 1 tree and indicates whether the tree was alive or dead (left axis) 2 years after the original census. The curves indicate the predicted annual mortality rate (right axis) as a function of dbh. The gray curve pertains to liana-free trees and the black curve to liana-infested trees. A) Understory. B) Slow-growing shade-tolerant. C) Fast-growing shade-tolerant. D) Dry forest. E) Light-demanding. F) Long-lived pioneers. G) Intermediate-lived pioneers. H) Colonizing pioneers.

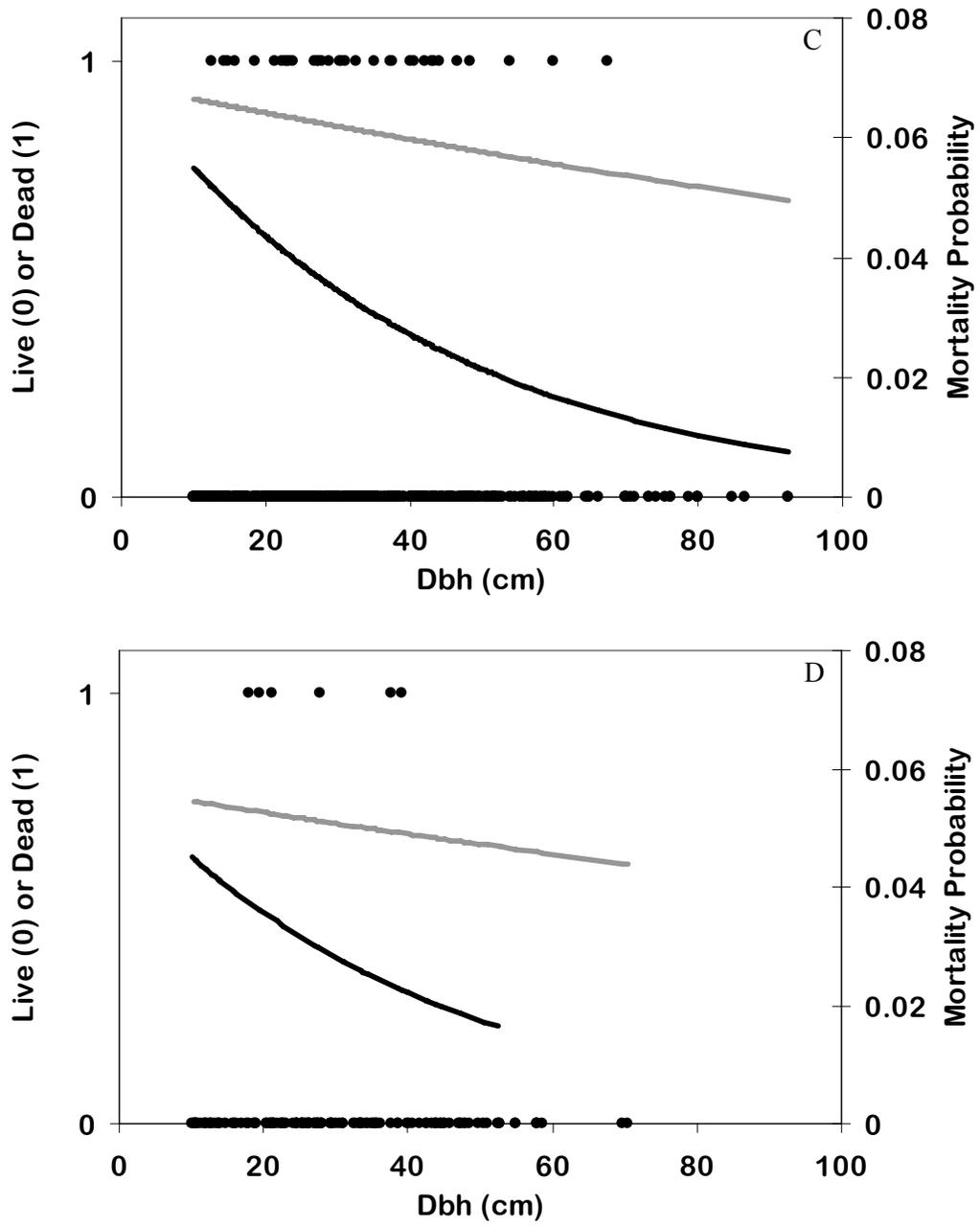


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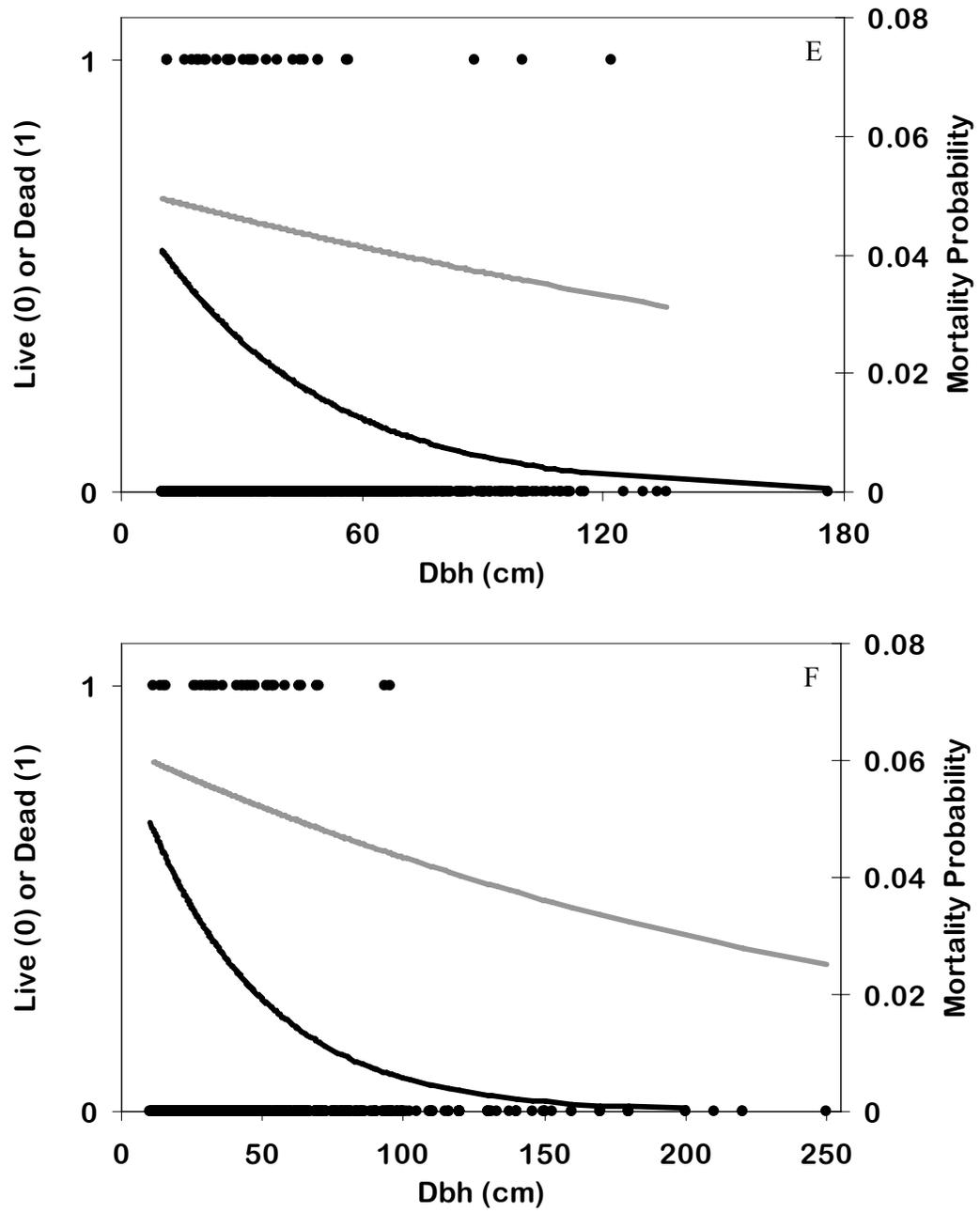
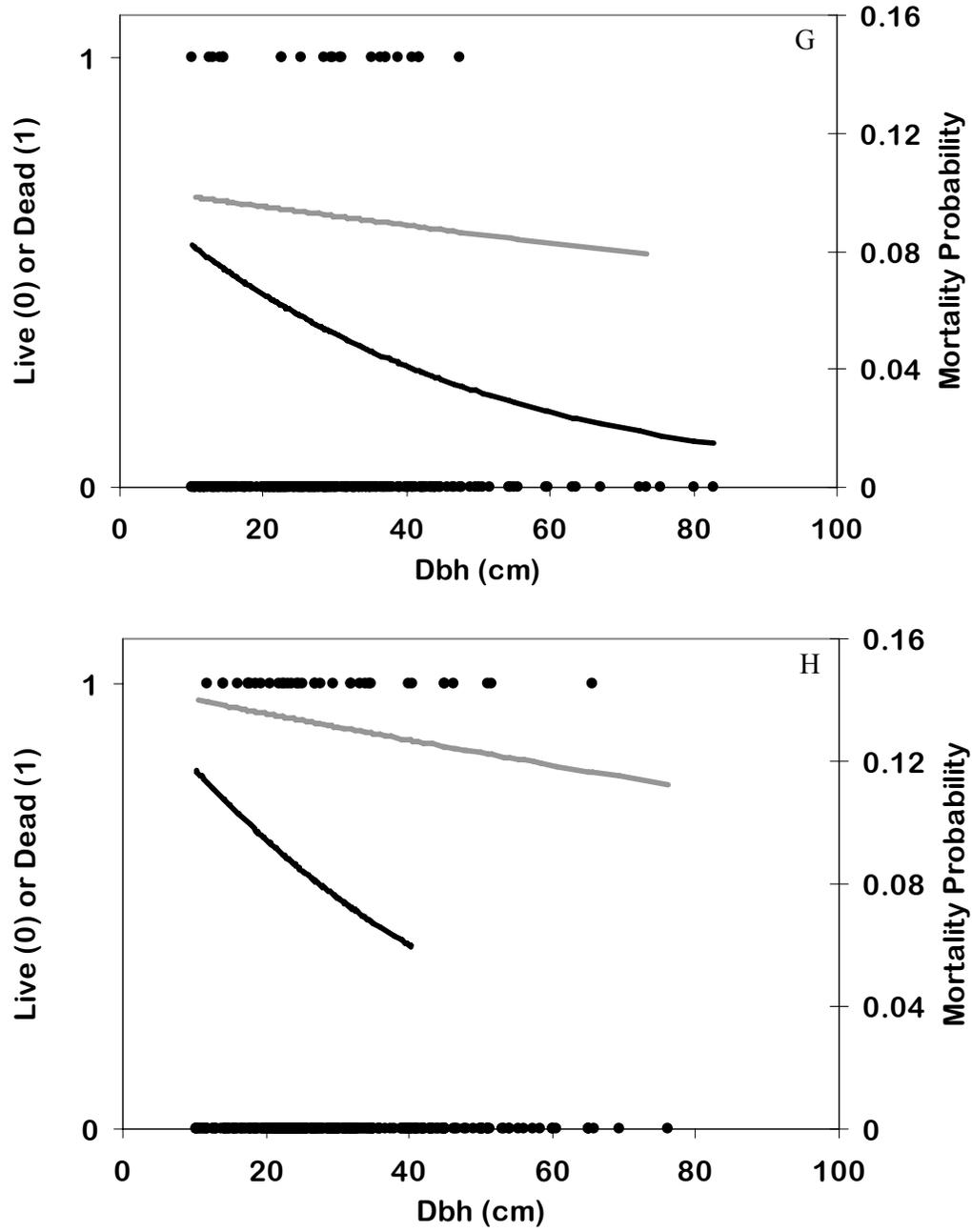


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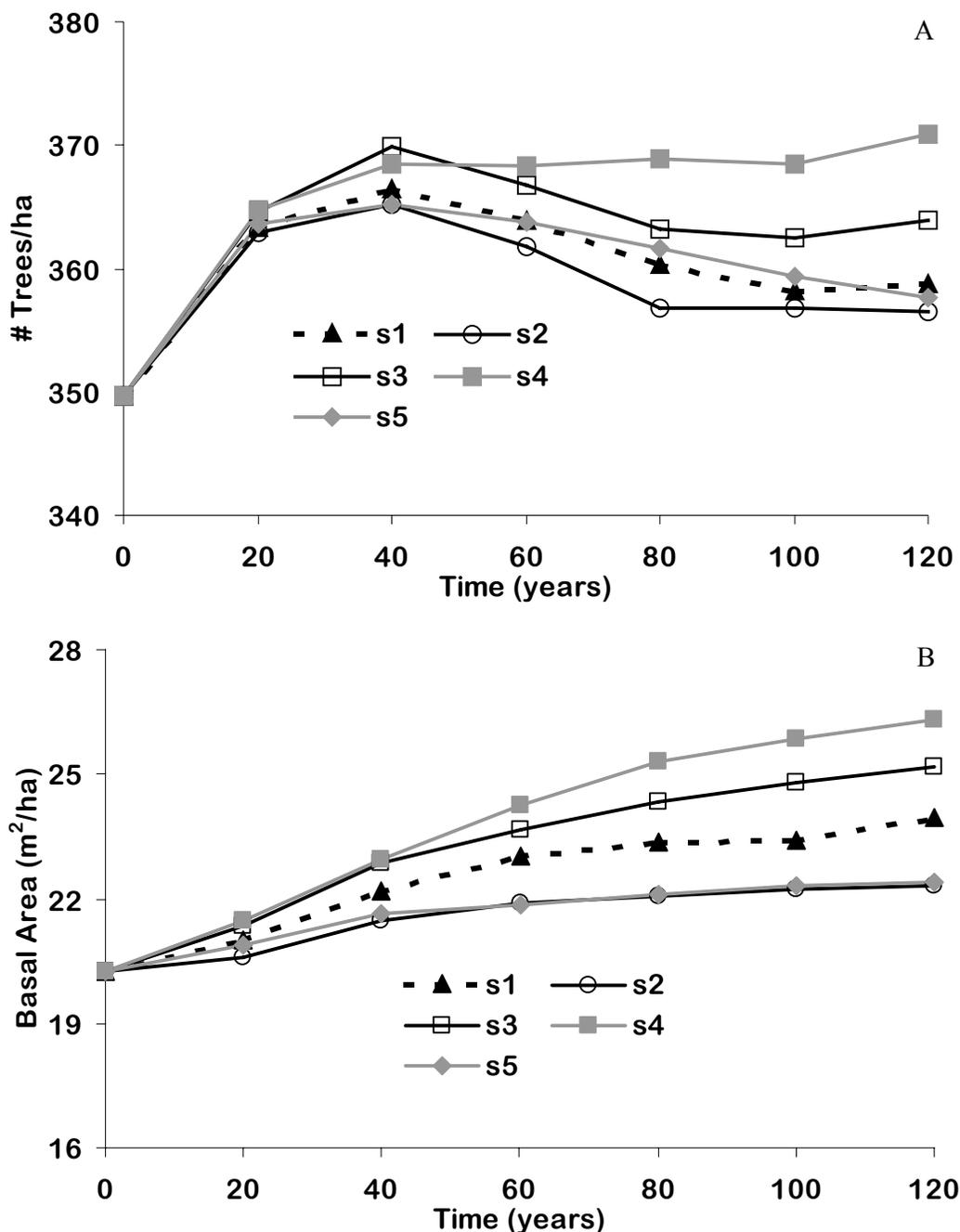


Figure 2-5. Sensitivity of total tree density and basal area to changes in mortality rates of large trees ($\text{dbh} > D_{95}$) as determined by the value of the supplemental mortality parameter (m_5) from Eq. 9. For each scenario (s1-s5) in the sensitivity analysis, m_5 was varied from the baseline values (s1) of 0.2 for colonizing pioneers and 0.05 for other species groups. For all species groups except the colonizing pioneers, the value of m_5 was increased by 50% in s2 or set equal to m_{95} in s3. When $m_5 = m_{95}$ there is no supplemental mortality. In s4, $m_5 = m_{95}$ for all species groups. In s5, $m_5 = 0.1$ for all species groups. A) Tree density (stems/ha). B) Basal area (m^2/ha).

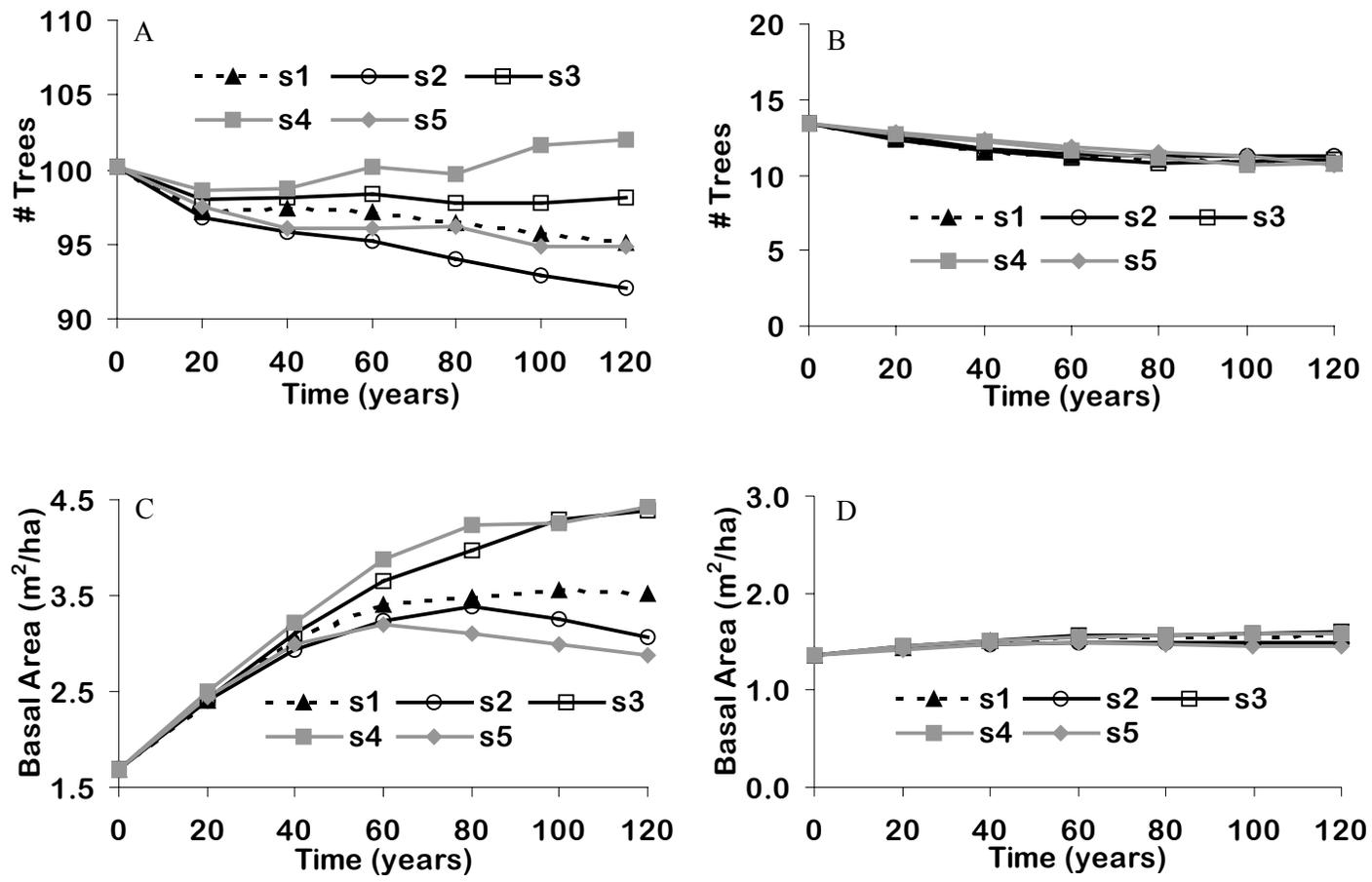


Figure 2-6. Examples of changes in tree density and basal area for species groups that were sensitive and insensitive to changes in mortality rates of large trees (dbh > D95) in La Chonta. A) Tree density sensitive: slow-growing, shade-tolerant species. B) Tree density insensitive: dry forest species. C) Basal area sensitive: fast-growing, shade-tolerant species. D) Basal area insensitive: understory species. Scenarios were the same as in Figure 2-5.

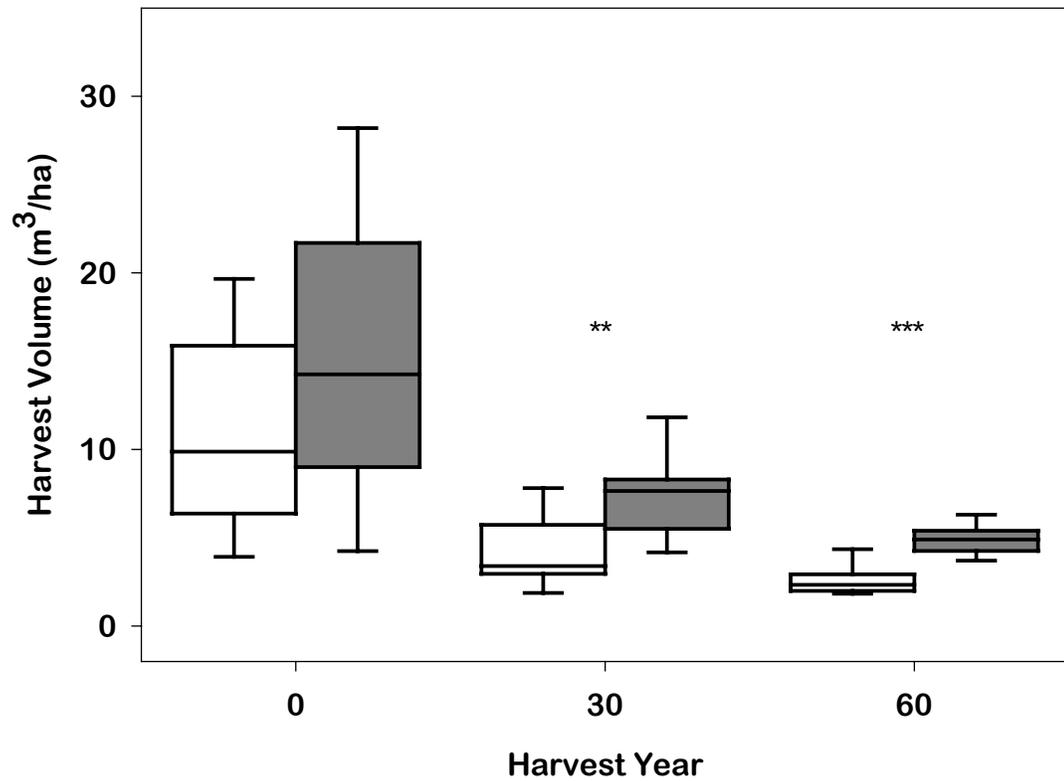


Figure 2-7. Harvest volumes obtained in years 0, 30, and 60 from the normal harvest and intensive management treatments in La Chonta based on simulations of 15 1-ha plots with 15 repetitions each. The double and triple asterisks above the boxes in years 30 and 60 indicate significant differences between the treatments at $P < 0.01$ and $P < 0.001$, respectively. The boxes indicate the quartiles, the line indicates the median, and the whiskers indicate the 10th and 90th percentiles of the observed harvest volumes. Errors are based on differences across the plots.

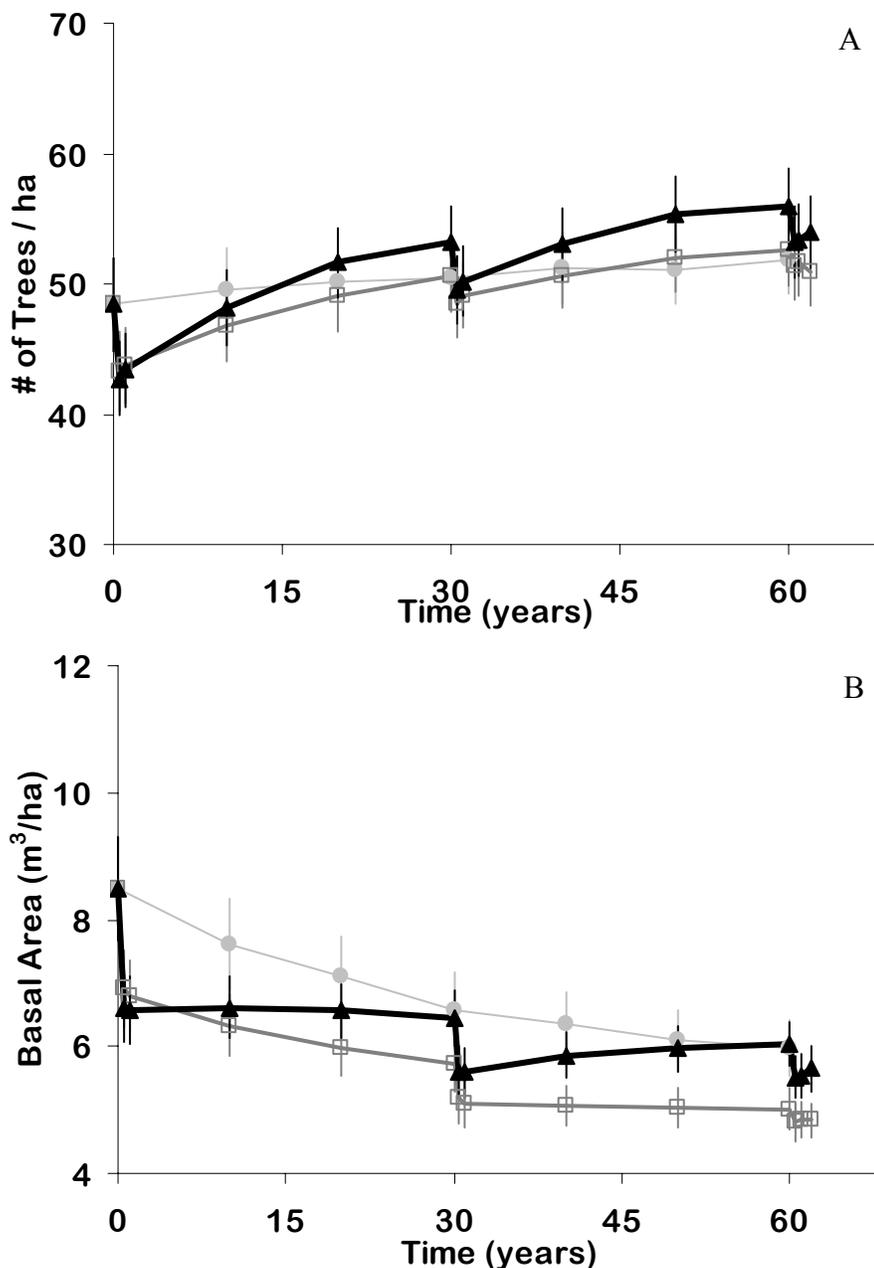


Figure 2-8. Simulated management treatment impacts on tree density and basal area by commercial class in La Chonta. A) Commercial species, tree density. B) Commercial species, basal area. C) Potentially commercial species, tree density. D) Potentially commercial species, basal area. E) Non-commercial species, tree density. F) Non-commercial species, basal area. Intensive management treatment: black triangles and lines. Normal harvest treatment: dark gray squares and lines. Control treatment: light gray circles and lines. Simulations run for 62 years and repeated 15 times for each of 15 plots. Error bars are standard error of the mean across the 15 plots. See Table 2-12 for a list of commercial and potentially commercial species. Note different y-axis scales.

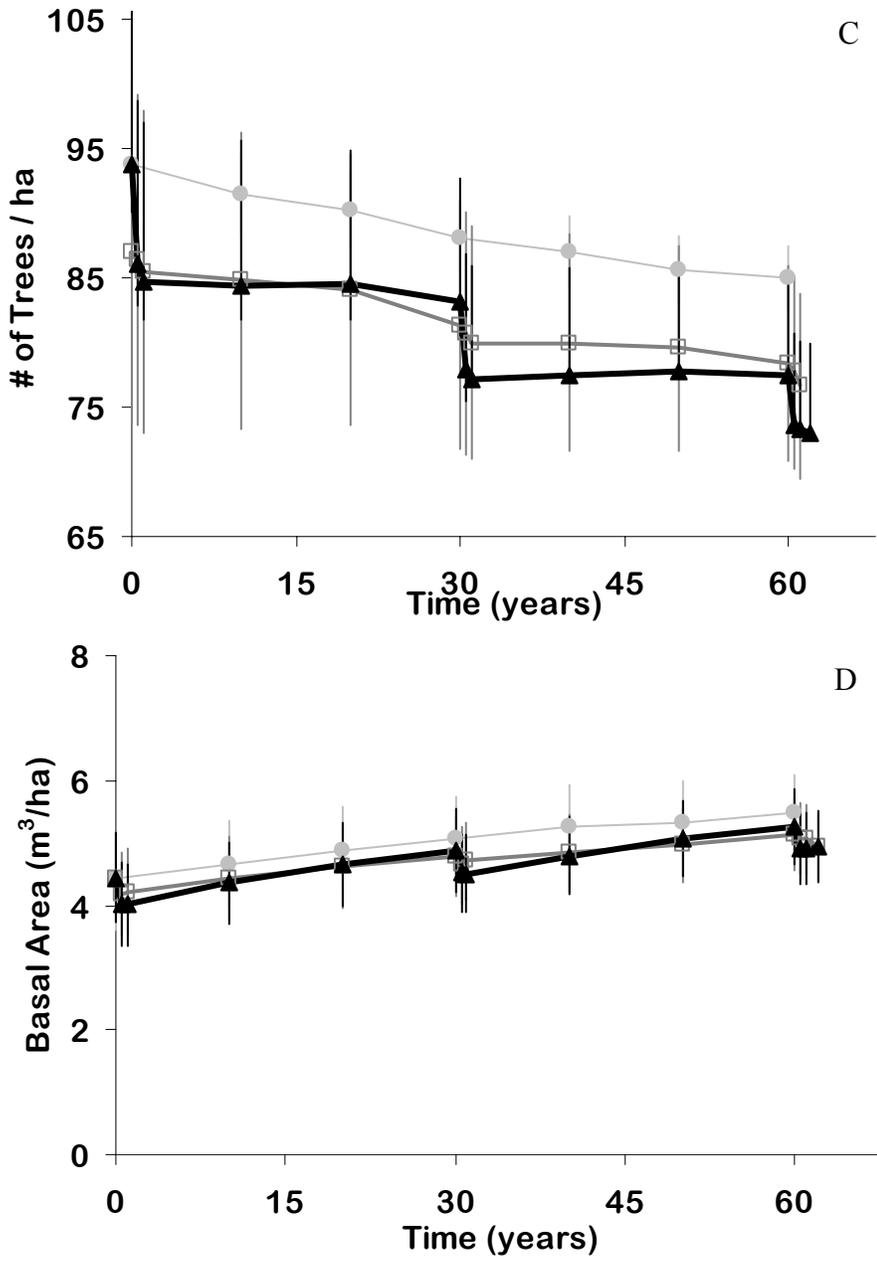


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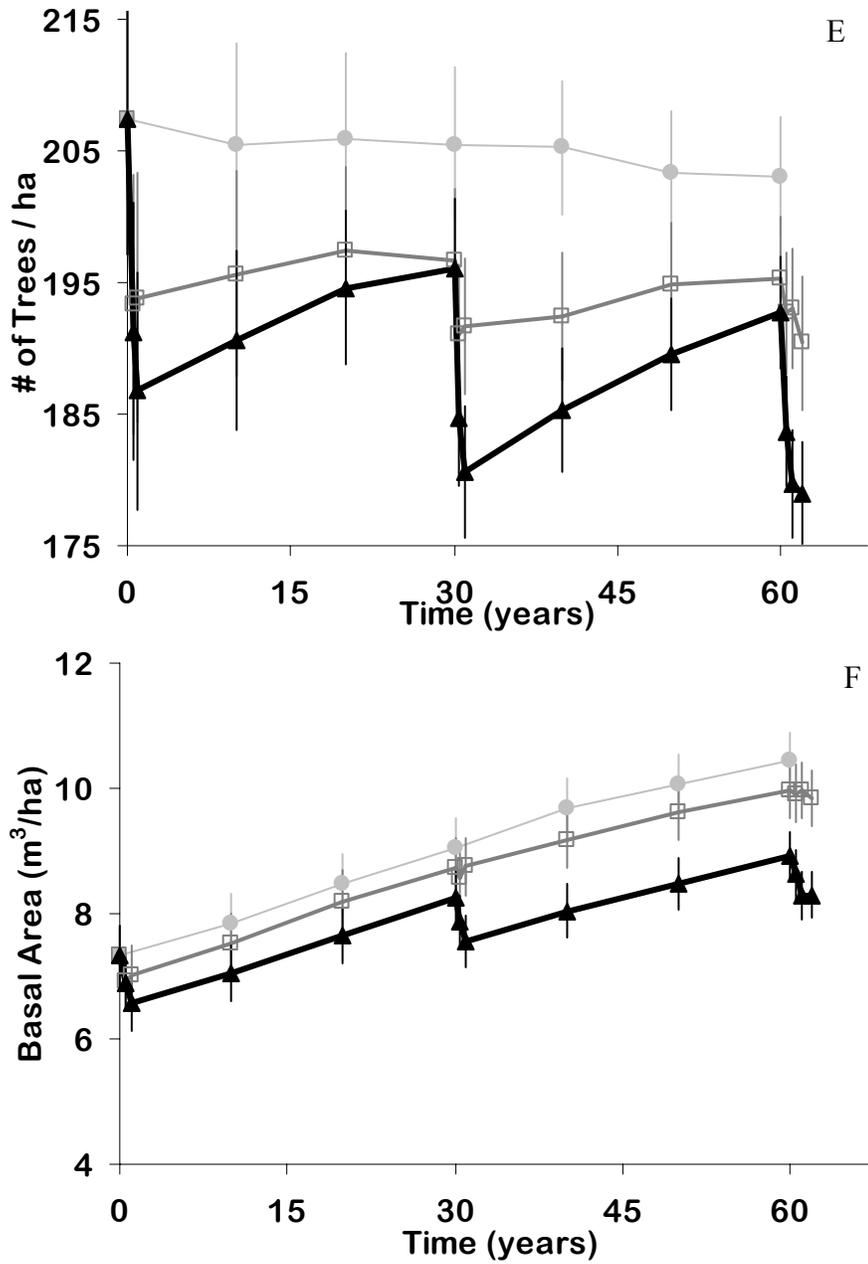


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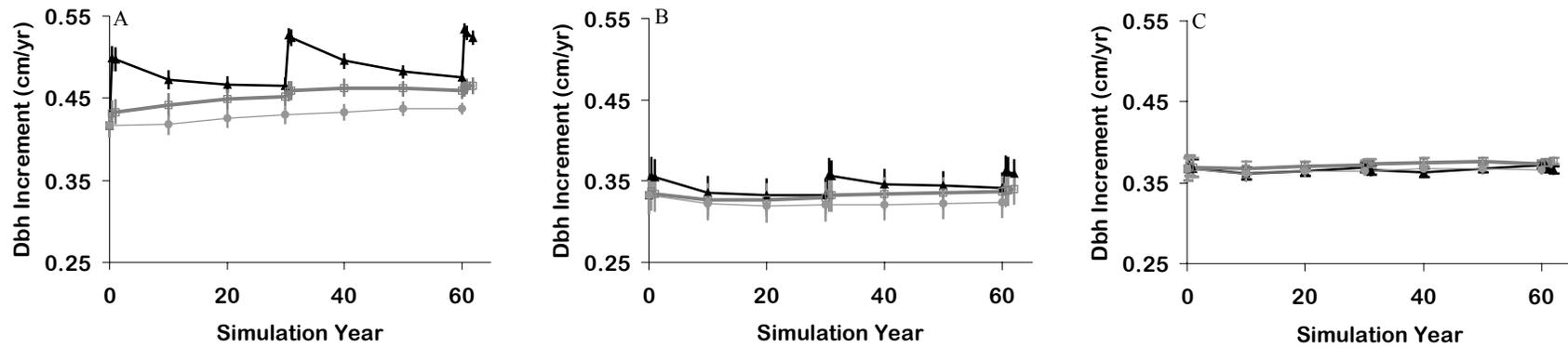


Figure 2-9. Diameter growth rates by commercial class observed in 62-year simulations of management treatments in La Chonta. Simulations were repeated 15 times for each of 15 1-ha plots. The normal and intensive management treatments included 3 cutting cycles at 0, 30, and 60 years. Intensive management treatment: black triangles and lines. Normal harvest treatment: dark gray squares and lines. Control treatment: light gray circles and lines. Error bars are standard error of the mean across the 15 plots in La Chonta. A) Commercial species. B) Potentially commercial species. C) Non-commercial species.

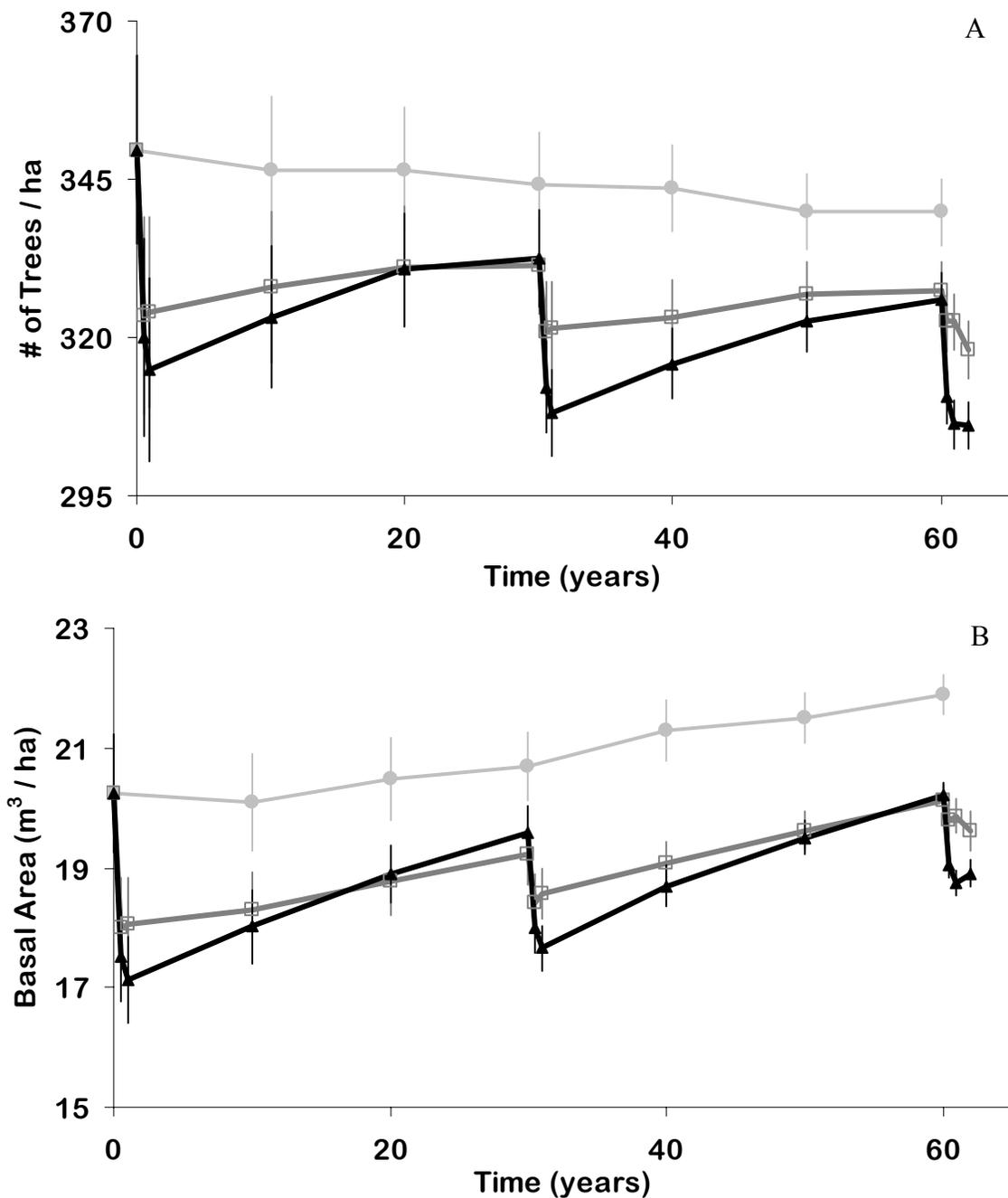


Figure 2-10. Changes in total tree density and basal area observed in 62-year simulations of management treatments in La Chonta. A) Tree density. B) Basal area. Simulations were repeated 15 times for each of 15 1-ha plots. Intensive management treatment: black triangles and lines. Normal harvest treatment: dark gray squares and lines. Control treatment: light gray circles and lines. Simulations included 3 cutting cycles in the normal and intensive management treatments at 0, 30, and 60 years. Error bars are standard error of the mean across the 15 plots in La Chonta.

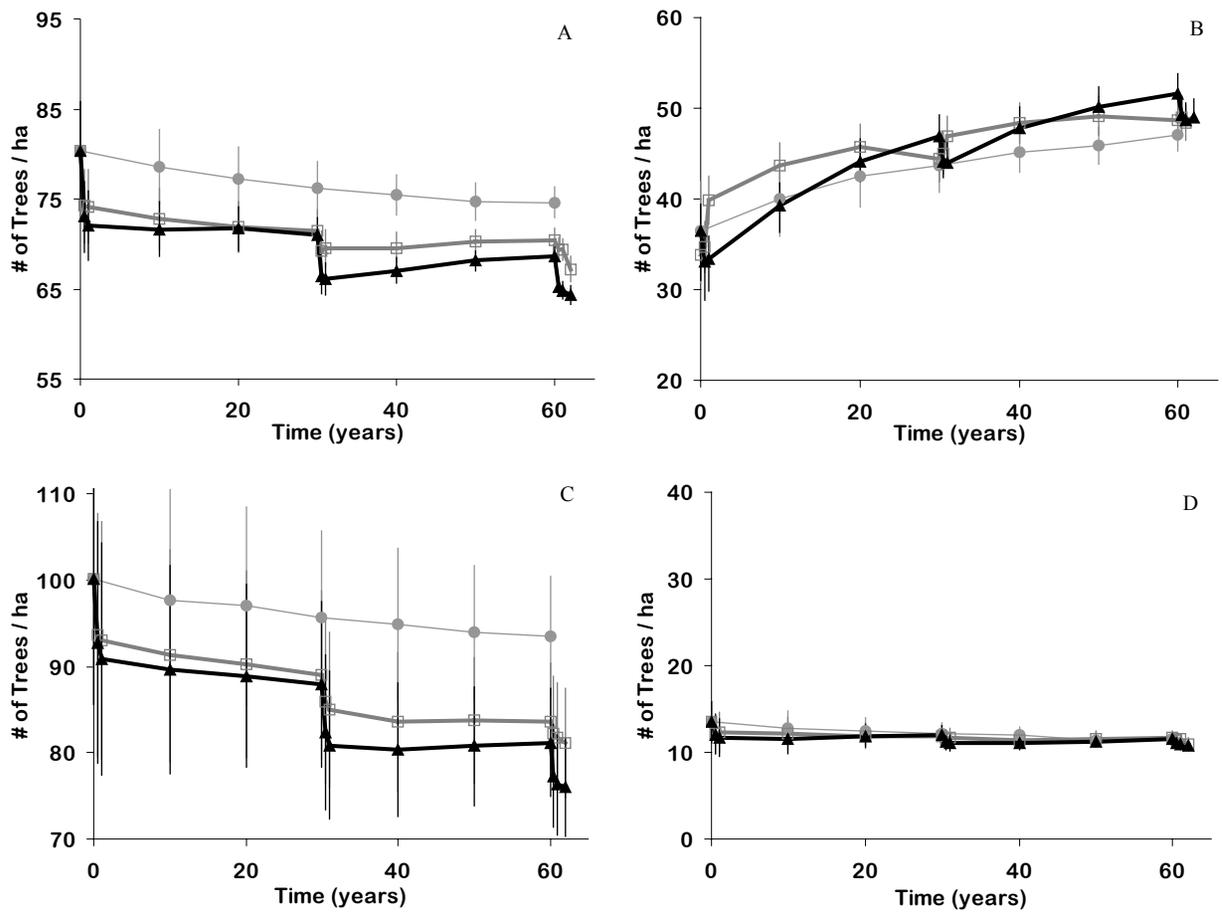


Figure 2-11. Species group-specific changes in tree density and basal area observed in 62-year simulations of management treatments in La Chonta. A–H) Tree density. I–P) Basal area. A and I) Understory. B and J) Long-lived pioneers. C and K) Slow-growing, shade-tolerant. D and L) Dry forest. E and M) Light demanding. F and N) Intermediate-lived pioneers. G and O) Colonizing pioneers. H and P) Fast-growing, shade-tolerant. See Figure 2-10 for explanation of symbols and Table 2-1 for species group details.

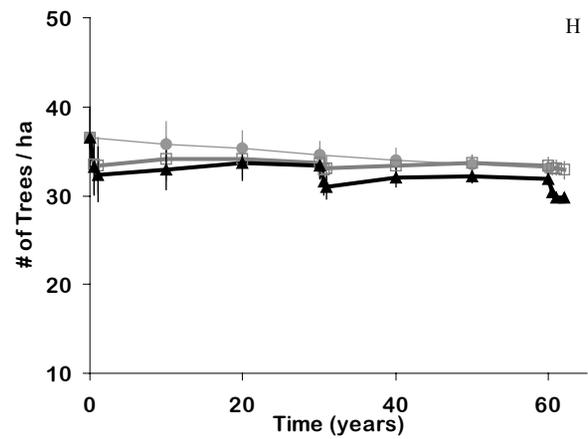
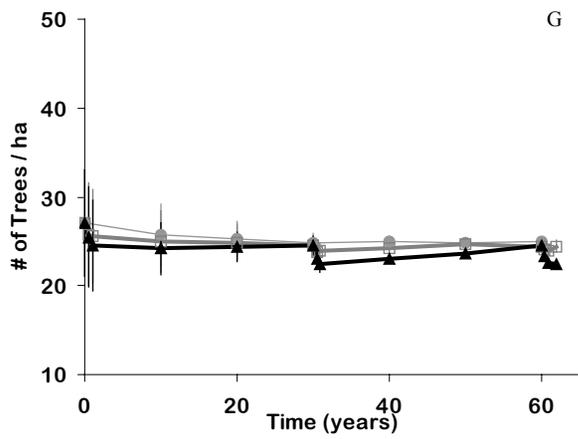
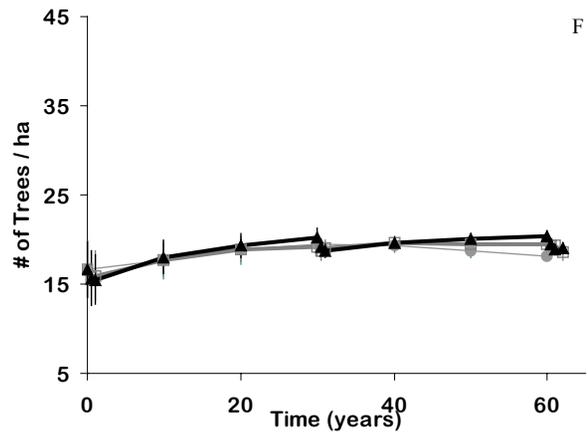
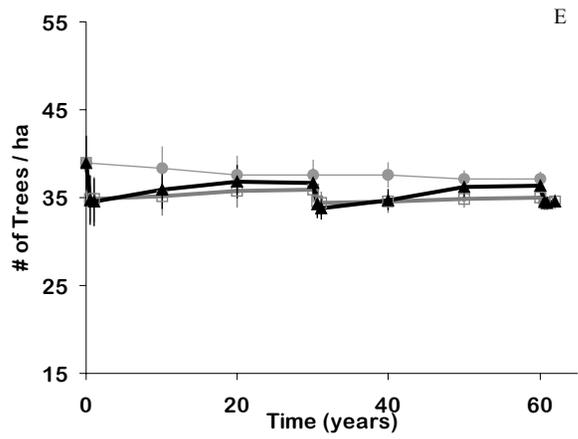


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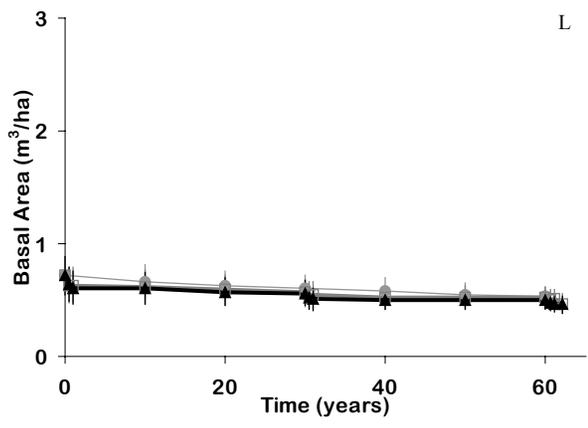
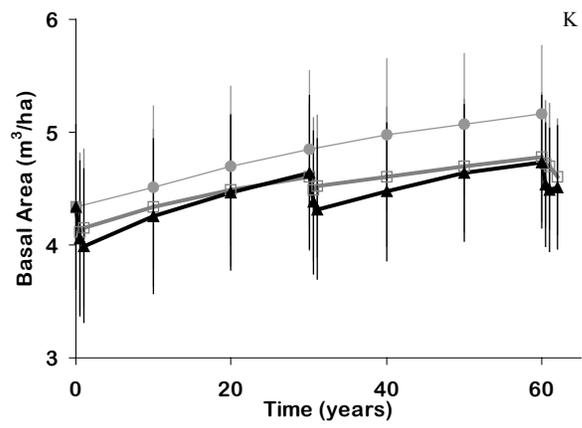
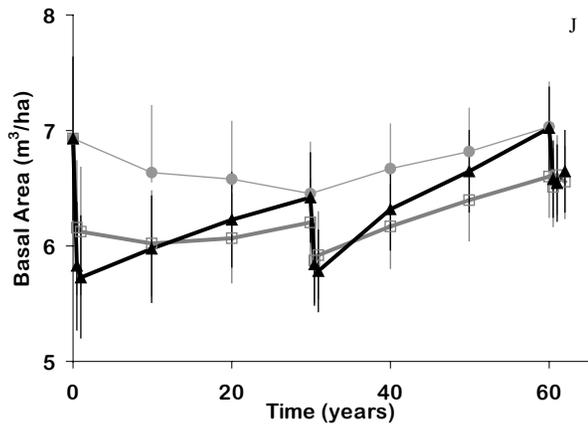
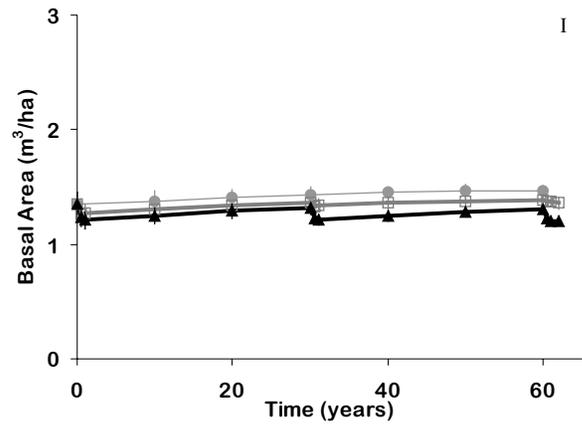


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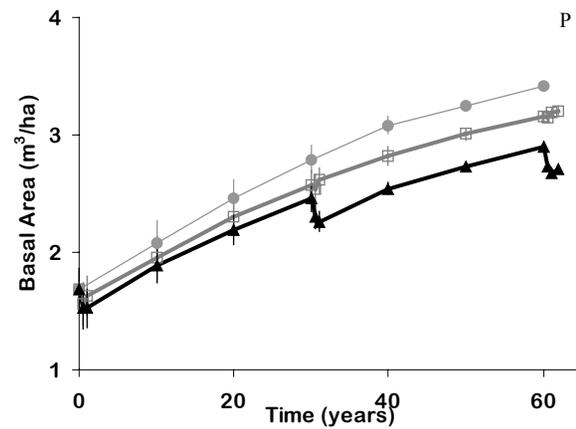
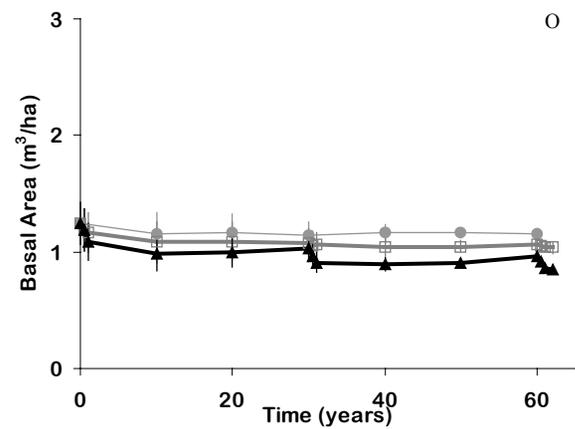
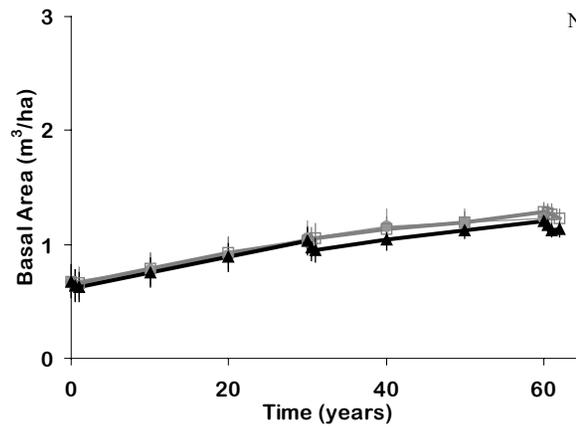
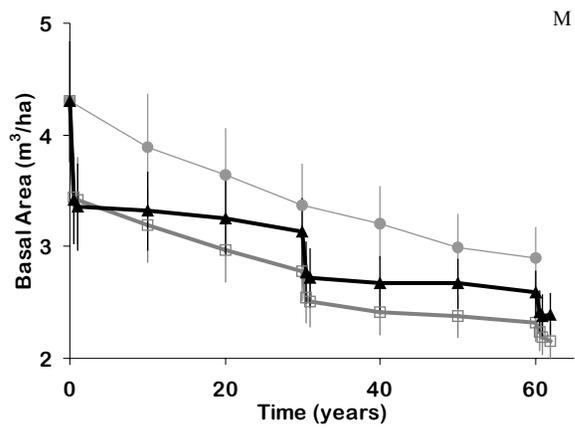


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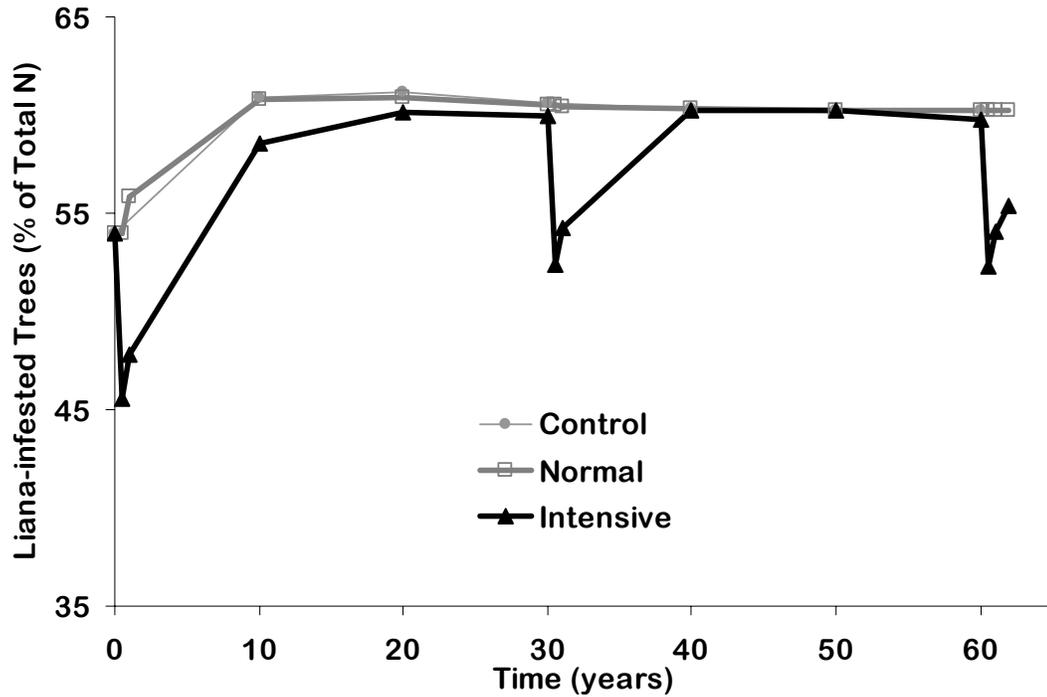


Figure 2-12. Changes in the proportion of trees with lianas observed in 62-year simulations of management treatments in La Chonta. Simulations were repeated 15 times for each of 15 1-ha plots. Intensive management treatment: black triangles and lines. Normal harvest treatment: dark gray squares and lines. Control treatment: light gray circles and lines. Simulations included 3 cutting cycles in the normal and intensive management treatments at 0, 30, and 60 years. Lianas were cut from crop and future crop trees before each harvest in the intensive management treatment only.

CHAPTER 3
TIMBER PRODUCTION, BIODIVERSITY CONSERVATION, CARBON
SEQUESTRATION, AND WILDFIRE TRADE-OFFS IN TROPICAL FORESTS

The earth belongs always to the living generation. They may manage it then, and what proceeds from it, as they please, during their usufruct. (Thomas Jefferson, south wall, Library of Congress)

. . . discounting means that any potential damages inflicted upon the next generation by the current generation are of almost no consequence, and we can delete the word “almost” in the previous phrase when referring to subsequent generations. (Toman and Ashton 1996, p. 344)

Introduction

Increasing concern about the dire local, regional, and global consequences of tropical deforestation has led to various strategies to conserve tropical forests (e.g., Archard et al. 2002). One key strategy, management for sustainable timber production, aims to increase the value of forests and thereby increase the probability of their conservation. This strategy is based on the findings of most financial analyses that timber is the most valuable product, and that timber management is usually the most lucrative use of public, private, and community owned forests (Pearce et al. 2003). Management for timber production (or any other sort of management) results in trade-offs both among different forest values and among stakeholders who place different values on the various goods and services forests provide. These trade-offs are important to clarify because perceptions and assumptions based on imperfect or limited information often drive individual and institutional decisions. A clearer understanding of the nature and magnitude of trade-offs at different scales should lead to better, or at least more-informed forest policies and decision-making (Alavalapati and Zarin 2004). In this

chapter, I discuss the trade-offs among timber production, biodiversity conservation, carbon sequestration, and wildfire in tropical production forests.

Trade-offs in Tropical Forest Management

Forest managers have long recognized that trade-offs among the goods and services forests provide inevitably result from any management decision (e.g., Dana 1943, Hartman 1976, Boscolo and Buongiorno 1997). Indeed, these resources accrue at different temporal and spatial scales to different stakeholders whose values and management objectives may be mutually exclusive in time, space, or both (Shea 1993, Toman and Ashton 1996). In recent decades, the growing number of stakeholders concerned with forest outcomes has multiplied the set of benefits that forest managers must attempt to provide simultaneously. The resulting debate over how to best conserve and use the earth's remaining tropical forests centers on the trade-offs among these stakeholders as well as the trade-offs among the myriad values and services forests provide.

Efforts to harmonize disparate management objectives have advanced substantially in temperate forests (e.g., Carey et al. 1999, Johnson et al. 2002, Stevens and Montgomery 2002), but harmonization has lagged in the tropics. A notable exception is the study by Maass et al. (2005) in which they assess trade-offs among ecosystem services and among stakeholders in a watershed scale study of the potential for sustained delivery of ecosystem services in western Mexico. Most other assessments of trade-offs among competing tropical forest management objectives seek to optimize combinations of outputs for economic efficiency, which is generally achieved when the net present value (NPV) of the forest is maximized. This approach has been used to assess trade-offs between timber and non-timber forest products (NTFPs, Ashton et al. 2001), timber and

biodiversity (Ingram and Buongiorno 1996), timber and carbon sequestration (Boscolo et al. 1997), and among timber, carbon, and biodiversity (Boscolo and Buongiorno 1997). A related approach—the production possibilities frontiers (PPF) model—has also been used to identify tropical forest management strategies that minimize trade-offs by optimizing combinations of various goods and services (Boscolo and Buongiorno 1997, Boscolo et al. 1997, Rohweder et al. 2000).

The PPF model distinguishes between joint production relationships that are incompatible, competing, or complementary (Figure 3-1a, cf. Rohweder et al. 2000). In an incompatible relationship, increased production of one good, such as timber, causes a rapid decline of the other good (concave curve in Figure 3-1a), such as the amount and quality of forest interior bird habitat (reviewed in Fimbel et al. 2001). In a competing relationship, the two goods are inversely proportional such that an increase in production of one good causes a slower decline in the other (convex curve in Figures 3-1a and 3-1b). This relationship has been observed in the tropics for timber production and carbon sequestration (Boscolo et al. 1997), and timber production and tree species diversity. A complementary relationship is where two activities may thrive simultaneously such as an increase in food resources for ungulates in response to timber production (Rohweder et al. 2000).

The PPF model is useful because it reveals the nature and magnitude of trade-offs and indicates the extent to which those trade-offs can be mitigated with alternative management strategies (Figure 3-1b). The biophysical joint production limits of two competing objectives (e.g., timber production and carbon sequestration) can be graphically represented by a curve (i.e., the frontier, Figure 3-1b). Theoretically, all

points along and below the frontier are joint production possibilities. Movement towards the frontier from inside the curve represents increased joint production, whereas movement along the frontier represents different optimum levels of joint production that different stakeholders may prefer depending on their perspectives and the distribution of benefits and costs. In contrast, any movement away from the frontier implies greater trade-offs.

Although NPV and PPF are indispensable for assessing trade-offs among forest management objectives, they should be informed by ecological analyses that determine whether the production possibilities are sustainable, and by sociological analyses that make explicit the distribution of benefits and costs among stakeholders (Alavalapati and Zarin 2004). NPV and PPF analyses by themselves are often limited because they require assumptions about the value of competing objectives and discount rates (i.e., the interest rate used to determine the present value of a future benefit), and usually do not explicitly consider more than one of the affected stakeholders. In addition, most of the dimensions that mediate forest management trade-offs should not be plotted as being orthogonal. Other important trade-offs of forest management, such as increased risk of fire following logging in closed tropical forests, do not fit into the general typology presented above because timber harvesting intensity, fire susceptibility, and fire intensity are generally positively correlated (Cochrane 2003, Chapter 1).

The nature and magnitude of forest management trade-offs depend on various factors including the forest itself (i.e., soil fertility and forest structure, composition, and dynamics), stakeholder values, management options and intensities, temporal and spatial scales, and discount rates. For example, the task of assessing trade-offs is greatly

complicated by the multitude of values and objectives held by different stakeholders as well as by the risks forest managers or owners face due to lack of secure land tenure, and the consequences of poor frontier governance such as illegal logging and fire (Nepstad et al. 2002). Time scales and discount rates complicate analyses because different stakeholders hold different perceptions of (and assumptions about the value of) intra- and intergenerational equity and the associated social and personal discount rates (Brennan 1995, Weitzman 1998).

In tropical countries that still have substantial forest cover, the continuing debate among environmentalists over the potential for forests managed for timber production to contribute to conservation goals (e.g., Rice et al. 1997, Romero and Andrade 2004) seems to hardly acknowledge that most remaining forests are outside of protected areas and are being cleared at undiminished rates (Archard et al. 2002). This crisis demands that the focus should be on how to maintain as much of the remaining forest as possible. More protected areas will certainly help (Bruner et al. 2001, Peres 2005), and innovative schemes such as payments for environmental services (PES) seem promising in certain cases (Balmford and Whitten 2003, Wunder 2005), but these strategies alone will not be sufficient to conserve all biodiversity, especially when one considers that nearly 25% of the remaining tropical forest area belongs to communities (White and Martin 2002, Molnar et al. 2004). Furthermore, although the net present value (NPV) of forest management for sustained yields (STY) is typically lower than for other options (Rice et al. 1997, Pearce et al. 2003), governments recognize the need to maintain forests, but wish to do so through environmentally sound and socially acceptable use (Boscolo and Buongiorno 1997, Poore 2003).

The international community has expended substantial resources seeking socially just ways to achieve conservation and development goals. Some of this effort has focused on making timber management more compatible with biodiversity conservation and other socially desirable goals, especially poverty alleviation and carbon sequestration to mitigate climate change resulting from anthropogenic greenhouse gas emissions (e.g., Wunder 2005).

Central to the promotion of management for timber production as a means to conserve tropical forests is the premise that they will be cleared for other uses wherever the opportunity costs of maintaining forests are too high. Deforestation patterns and trends throughout the tropics seem to substantiate this premise. Considering that both accessibility (Kaimowitz and Angelsen 1998) and the value of other possible land uses influence whether forests remain standing, it is critical to maximize the value of remaining forests through a combination of forest management aimed at securing STY, timber certification, NTFP production, and PES. If accessible forests on good soils are still converted to other uses despite achieving this goal, it could be argued that the forest was not adequately valued. Although it is premature to be optimistic about the prospects of forest management to live up to the expectations of the international community, examples of good management are becoming more abundant, as indicated by the growing area certified as well managed by the Forest Stewardship Council (FSC; www.fsc.org).

Focus on Timber, Carbon, Fire, and Biodiversity

My analysis focuses on trade-offs among stand management for sustained timber yields (STY), carbon sequestration, biodiversity conservation, and fire susceptibility and intensity. My justification for focusing on timber production is that despite the continued low price of most tropical woods (a problem exacerbated by illegal wood saturating

markets) timber remains the most valuable tropical forest commodity (Pearce et al. 1999). The focus on carbon and biodiversity are justified because they are globally important values; tropical forests are well known as the earth's greatest repository of biodiversity and for their critical role in moderating the global climate. Furthermore, both biodiversity and carbon sequestration potential are affected in complex ways by efforts to secure STY. Additionally, the carbon storage function of tropical forests may be second only to timber in terms of financial value (Pearce et al. 2003). When compensation for the carbon value is included in analyses of forest harvesting decisions, for example, reduced-impact logging (RIL) techniques become financially viable (e.g., Pinard et al. 2000, but see Healey et al. 2000 vs. Holmes et al. 2002).

Fire is becoming increasingly prevalent even in non-fire adapted forests previously thought to be impervious to fire (Goldammer 1990, Cochrane 2003, Barlow and Peres 2004). Whereas previously fire risks were acknowledged for seasonally dry tropical areas with deciduous or semi-deciduous forests, abundant buried charcoal throughout the Amazon indicates that fires occurred but at several hundred year intervals in wetter, evergreen forests (Sanford et al. 1985, Saldarriaga and West 1986). The fires that have devastated large forest tracts throughout the tropics in the past two decades, in contrast, make it clear that most tropical forests, logged or unlogged, are now very fire prone (Siegert et al. 2001, Cochrane 2003, Chapter 1). Considering that global warming is expected to cause more frequent and prolonged droughts (Timmerman et al. 1999), the susceptibility of tropical forests to fire will only increase (Cochrane 2003, Barlow and Peres 2004) especially as the remaining forests become more fragmented as a result of land use changes, road building, and migration (Nepstad et al. 2001, Laurance 2003).

Aside from the consequences of these fires for biodiversity and climate change, the negative effects of the smoke from these fires on human health and commerce are substantial (Nepstad et al. 1999a), with an estimated 75 million smoke-related medical complaints from the 1997–98 Indonesian fires alone (CIFOR 2001, p. 32).

The Silvicultural Challenge of Achieving STY in Tropical Forests

Foresters face many challenges in trying to achieve STY in most tropical forests. The characteristically high tree diversity means that most species occur at low densities. Furthermore, commercial tree species often vary substantially in their silvicultural requirements. The lack of regeneration and slow growth rates typical of many commercial species further complicate the forester's task. Even where future crop trees (FCTs) are abundant (e.g., dipterocarp forests), STY has been elusive due to over-harvesting, poor supervision, and lack of trained personnel, as well as social and political factors (e.g., greed, graft, corruption, and lack of governance). In drier, seasonally deciduous tropical forests, stocking of commercial species with adequate markets is often poor and the cutting cycles are shorter than the time needed for slow growing trees to reach the minimum dbh (diameter at 1.3 m) for felling (Dauber et al. 2005). Moreover, many of these forests have high liana densities (Alvira et al. 2004), which further slow growth, increase mortality, and impede succession. The high susceptibility to fire of these drier forests, increasingly frequent and prolonged El Niño-associated droughts, and somewhat open canopies due to high-grading or previous fires, further challenge tropical forest managers.

Promoters of tropical forestry have long argued that silvicultural treatments beyond RIL are necessary to achieve STY (Dawkins and Philip 1998, Wadsworth 1998). While this conclusion seems generally true, results from field and simulation experiments in the

dipterocarp forests of SE Asia suggest that STY can be achieved if harvested volumes are modest and RIL is implemented by crews that are well trained and supervised (Pinard and Putz 1996, Sist et al. 1998, Pinard and Cropper 2000, Huth and Ditzer 2001, Phillips et al. 2003). The silvicultural treatments typically recommended for tropical forests include removal of lianas from FCTs and killing non-commercial trees competing with FCTs to accelerate their growth (e.g., Fredericksen and Putz 2003). In some cases, enrichment planting and soil scarification have successfully enhanced regeneration of light-demanding species (Negreros-Castillo et al. 2003, Snook and Negreros-Castillo 2004).

At first glance, it would seem that intensive silviculture diminishes the carbon and biodiversity values of the forest while rendering it more vulnerable to catastrophic fire, but understanding these trade-offs warrants inspection and consideration from a variety of perspectives. Obvious considerations include logging intensity, the proportion of forest area affected by silvicultural treatments, wood densities and tree growth rates, and the impact of reduced biomass on weed infestations and forest dynamics. The timber and biodiversity trade-offs also depend on the components or attributes of biodiversity studied, the landscape matrix surrounding the studied forest, and the relative importance of direct and indirect effects of silvicultural treatments. A less obvious consideration is the tacit assumption that pre-European or immediately pre-intervention forest structure and composition is somehow sacred and must be retained or restored. This assumption has been increasingly questioned as evidence of extensive human intervention in most tropical forests mounts (Denevan 1992, Foster et al. 1999, Bayliss-Smith et al. 2003, Heckenberger et al. 2003, van Gemerden et al. 2003, Johnson 2005, Miller et al. 2005).

Despite the numerous social, political, and economic trade-offs of timber production, carbon sequestration, biodiversity conservation, and fires in tropical forests, I restricted this study to biophysical trade-offs and addressed the following questions:

- How does intensifying management to achieve STY affect
 - Timber production,
 - Forest structure and composition (and other biodiversity measures for select taxa),
 - Carbon sequestration, and
 - Fire susceptibility and the intensity of fires that occur?
- To what extent can the results found be generalized to different tropical forests?
- What adjustments to forest policy and/or management guidelines should be undertaken in light of the results found here?

Approach

General Approach

A large quantity and variety of data are needed to assess the tradeoffs in biodiversity conservation, carbon sequestration, and fire susceptibility and intensity that result from management to achieve STY. Many of the data necessary to quantify the biophysical aspects of these trade-offs can be derived from permanent plots established to investigate forest dynamics. These data can be used to parameterize simulation models capable of evaluating the effectiveness of different management options in achieving STY as well as their impacts on biomass and carbon sequestration potential. Additional data on wood specific gravity and height-dbh relationships are also needed to estimate tree biomass, which typically comprises >75% of total aboveground biomass (Brown 1997, Nascimento and Laurance 2002). Permanent tree plot data coupled with additional information on target taxa provide a basis for assessment of the impacts of intensive

management on biodiversity (at least at the community and population levels). To assess the fire susceptibility and intensity trade-offs, data are needed on the impacts of different management intensities on fuel loads, fuel dry-down rates, and microclimate so that simple models of fire susceptibility can be used to predict when and for how long a forest is fire prone after management treatments are applied. Finally, data on regional shifts in land-use, prevalence of fire in the landscape, and regional climate change predictions will also help explain changes in fire susceptibility and intensity resulting from the management strategies being compared.

This analysis centers on the case of La Chonta, a certified timber concession in the seasonally dry transitional forests of lowland Bolivia for which I have collected enough data to make an initial assessment. My trade-off assessments include: (i) a review of the data available for La Chonta on the impacts of logging on forest structure and wildlife; (ii) a summary of field experiments that determined the impacts of different management intensities on correlates of fire susceptibility and intensity (Chapter 1); and, (iii) a summary of the results of model simulations that quantified potential future harvest volumes and carbon storage in response to different management intensities. I simulated forest changes for only a relatively short period of time (60 years) because predicting the long-term outcome of management treatments with confidence is difficult especially for tropical forests in a non-equilibrium state. Then, to assess the applicability of this approach to assessing forest management trade-offs, I compare the results from La Chonta to wetter forests in the eastern Amazon and Southeast Asia.

Specific Approach: the Case of La Chonta

Site description

La Chonta is a 100,000 ha timber concession in Guarayos Forest Reserve (15°45'S, 62°60'W) in the Bolivian lowlands (200–400 m.a.s.l.). The concession is covered by tropical humid semi-deciduous forest with common species including Ficus boliviana, Hura crepitans, and Pseudolmedia laevis. Mean annual temperature is ~24.5 °C and mean annual rainfall is ~1,500 mm, 77% of which falls between November and April. Soils are moderately fertile inceptisols and 10–15% of the area has black anthrosols (Paz 2003). La Chonta's structure is quite open (30% in gaps or low stature forest) giving it the appearance of a secondary forest, although total basal area (for trees > 10 cm dbh) is about 20 m²/ha and the canopy dominants are large (attaining heights of 35–45 m and dbhs of 150–250 cm). Various parts of this forest were high-graded from 1977 until 1996 for mahogany (Alvira et al. 2004), but this activity probably did not contribute greatly to La Chonta's present physiognomy. Most of the tree species dominating the canopy are light-demanding and lack regeneration (Mostacedo and Fredericksen 1999). The forest is extremely fire prone for ~132 days/year (Chapter 1). In 1995, 30% of the concession burned (Pinard et al. 1999a), and a 1999 fire destroyed huge areas of nearby forests and the town adjacent to the concession. Nevertheless, there were no signs of recent fires in my study area.

A silvicultural experiment comprising 4 treatments of increasing intensity in La Chonta was established in 2000 to explore the regeneration and growth of commercial tree species (IBIF 2004). The four management treatments included: “control” = no logging; “normal logging” = standard planned logging with no other silvicultural

interventions; “improved management” = “normal logging” with liberation of future crop trees from vines and overtopping non-commercial trees; and, “intensive management” = “improved management” with double the harvest intensity (as measured by the number of trees harvested), additional future crop tree liberation, and soil scarification in selected felling gaps. The improved and intensive treatments aimed to promote the regeneration and growth of commercial timber species, most of which are light-demanding (Mostacedo and Fredericksen 1999, Pariona et al. 2003). Evidence for the potential benefit of soil scarification on commercial regeneration was particularly strong: Fredericksen and Pariona (2002) found that Schizolobium amazonicum densities were nearly 10 times higher and height growth was twice as great in scarified vs. non-scarified felling gaps.

Management impacts on timber volumes

To evaluate the effectiveness of the different intensities of management in achieving STY, I used a simulation model (SYMFOR-see www.symfor.org and Phillips et al. 2002, Phillips et al. 2003, Phillips et al. 2004b) calibrated with data from a long-term silvicultural research experiment established in La Chonta in 2000 (see Chapters 1 and 2, IBIF web site). Although the model did not simulate fire susceptibility, it enables me to project the likely impacts of different management intensities on forest structure (including biomass) and composition as well as the potential harvest volumes of commercial species over a 60-year period (2 cutting cycles).

According to the model’s projections, none of the management intensities tested would achieve STY, but the most intensive management treatment would come closest (Figure 3-2). Regardless of the management strategy used, timber volumes were very low even by tropical standards (only 11–15 m³/ha in the first harvest) and hence impacts

on forest structure and composition were relatively modest (Chapter 2). Compared to under the normal (typical) harvesting scenario, timber yields under intensive management were greater by 43% in the first cut, 105% in the second cut, and 231% in the third cut (Chapter 2). In the second and third simulated harvests, the intensive management treatment volumes were 47% and 32%, respectively, of the volume obtained in the first cut. In contrast, harvested volumes of the second and third harvests under the normal treatment were only 33% and 14% of the first harvest. As explained in Chapter 2, the greater volumes harvested in the intensive treatment were not only attributable to the benefits of the silviculture, but also to the greater number of species harvested. To achieve STY, the cutting cycles need to be longer, silvicultural treatments need to be more intensive, and more species and/or smaller trees need to be harvested.

Stakeholder perspectives. The trade-offs resulting from efforts to achieve STY through intensive silviculture vary for different stakeholders. I briefly discuss these trade-offs for four broad groups of people with a stake in the fate of tropical forests: loggers and the timber industry with an emphasis on concessionaires; communities living near timber concessions; tropical governments; and the international conservation community. Because I did not collect data on the attitudes of these stakeholders, my conclusions are based on my own assumptions about stakeholder perspectives as well as those published elsewhere.

Loggers and the forest industry should be among the principal beneficiaries of efforts to secure STY. But whether and how much they benefit depends on the costs of implementing the necessary silvicultural treatments, and whether those costs can be recuperated (e.g., through higher wood prices). Whether and how much loggers benefit

also depends on the discount rate used to calculate the costs and benefits of the applied silviculture. An analysis of the costs and benefits of several of the silvicultural treatments applied in La Chonta indicated that the internal rate of return ranged from 10% to 18% (Evans et al. 2003). To the extent that intensive silviculture increases the forest's productivity or makes more efficient use of the forest's timber, it also should persuade these stakeholders to protect their investment (and hence the forest) over the longer term. Over the shorter term, they should also benefit because of the greater timber volumes harvested.

Although forestry work is dangerous and other livelihood options may be more attractive for various reasons, the intensive management treatment also should benefit local communities by providing more secure employment over a longer term. The greater, more sustainable supply of locally available wood resulting from intensive management should also benefit local communities.

Increased timber production from intensifying management benefits local municipalities as well as national governments. The principal immediate benefit would be increased revenues—assuming royalties, taxes, or stumpage fees could be adequately captured—due to increased timber volumes harvested. Eliminating corruption and making revenue collection more transparent should make this process more effective.

The conservation community might be considered the stakeholders who would bear the greatest costs of increased timber production from intensive silviculture because of the impacts on biodiversity, carbon, and fire susceptibility and intensity. These trade-offs depend strongly on the assumption that the probability of forest conversion would decrease as management improves and moves closer to achieving STY. Considering the

results above, I further assume that the intensive management treatment or more intensive silviculture will be most likely to achieve that goal.

Management impacts on biodiversity

My assessment of the management treatment effects on biodiversity in La Chonta is based on forest structure and wildlife species richness and abundance. First, I used projected changes in forest structure and composition from the SYMFOR model mentioned above and described in detail in Chapter 2. Second, I compiled results from studies conducted in La Chonta and nearby forests that examined the impacts of logging on a variety of taxa (Table 3-1).

Forest structure and composition. A post-harvest damage assessment in La Chonta found that although only 3–5 trees/ha (11–18 m³/ha) were harvested (IBIF 2004), about 50% of the area was disturbed, and the average felling gap area was 224 m² (range: 36-1091 m², Ohlson-Kiehn et al. 2003). In the SYMFOR simulations, 22 to 24 trees were fatally damaged per ha (i.e., about 7 trees \geq 10 cm dbh killed for each tree harvested).

These management impacts must be viewed in the context of La Chonta's pre-treatment forest structure and potential for recovery. Specifically, it is important to note that 30–37% of the unlogged forest in La Chonta was in gaps and building phase (i.e., low stature forest, Chapter 1). Moreover, the intensive management treatment decreased tree basal area (trees \geq 10 cm dbh) by only 15% and tree density by about 10% (Chapter 2). The additional silviculture applied in the intensive management treatment was also quite selective: only 4–6 trees/ha were killed by poison-girdling, only 30% of felling gaps were scarified, and vines were cut from only about 26 future crop trees/ha. Finally, the simulation results indicated that the forest would recover most of its basal

area within 30 years at the management intensities applied (Chapter 2), suggesting that it may be resilient to more intensive silviculture as well.

Although it is too early to make definitive statements about the effects of intensifying management on tree species composition, the simulation results offer some likely possibilities. The results suggest that major changes in species composition are unlikely over the 60-year simulation period, at least at the management intensities tested. Nevertheless, the post-harvest decreases in density and basal area observed for the commercial dry forest and light-demanding tree species groups (Chapter 2) suggest that without additional silviculture to secure regeneration and boost recruitment, these species groups would probably not recover their pre-harvest densities or basal area.

Wildlife impacts. The studies conducted in La Chonta that assessed the impacts of logging on wildlife reveal what others across the tropics have shown: the impacts depend to a great extent on the taxa studied (reviewed in Putz et al. 2000, Azevedo-Ramos et al. 2005, also see Table 3-1). For example, although bird species associated with interior forest habitat, such as canopy insectivores and near-ground omnivores, were most abundant in areas apparently unaffected by previous fire or logging, other guilds were more abundant in the disturbed areas of La Chonta (Woltmann 2003). A different study found that bird species considered interior forest specialists were equally abundant in logged, burned, and undisturbed areas (Flores et al. 2001). Similarly, Fredericksen and Fredericksen (2002) found that although logging decreased canopy cover by 24%, the abundance of the herpetofauna was the same as in unlogged forest whereas small mammal abundance and richness and terrestrial invertebrate abundance were all higher in areas disturbed by logging. Herrera-Flores (2003) also found that for most mammal and

bird guilds the magnitude of the management treatment impacts applied in La Chonta was small and whether population densities increased or decreased depended on the individual species. Finally, Quiroga and Herrera-Flores (2003) found that management treatment effects depended on interactions among guilds, animal body sizes, seasons, and the areas sampled. For example, capture rates and richness of small, non-volant mammals were greater during the rainy season and in the more intensively disturbed areas, but these differences depended on the logging unit sampled.

Although other components and attributes of logging impacts have yet to be studied in detail in La Chonta, it seems reasonable to conclude that the direct physical impacts of silviculture are less detrimental to wildlife (at least at the population level) than the indirect effects, especially hunting and fire. For example, exclusion of hunting in La Chonta has prevented the local extirpation of some wildlife species with dwindling populations (personal observation). Local abundance of tapirs, for example, has actually jeopardized the results of some regeneration enrichment experiments (M. Peña-Claros, personal communication). Thus, the hunting prohibition and fire prevention are likely to be the most important management interventions for conservation of wildlife (Rumiz et al. 2001). It is difficult to predict whether these conclusions would remain valid if silvicultural intensities were increased sufficiently to achieve STY. But, various management strategies—such as setting aside core refuge areas and/or spatially arranging annual harvest units so that source-sink areas could be left relatively intact (Fimbel et al. 2001)—could be implemented to mitigate the increased physical effects of doing so.

Stakeholder perspectives. Over the short-term, loggers and the forest industry do not bear the costs of the biodiversity impacts. These stakeholders may even benefit to

some extent if the relative abundance of the commercial tree species increases as a result of intensive management. Forest owners, concessionaires, and loggers may receive direct benefits in the form of payments to mitigate the negative impacts on biodiversity. Over the longer-term, if the direct effects of silviculture (including harvesting impacts) substantially alter important functional attributes of biodiversity, such as pollination, dispersal, seed predation, and herbivory, forest composition may change in undesirable ways (from their perspective). Specifically, these stakeholders would be negatively affected if changes in these processes decrease growth, survival, or recruitment of commercial species.

It is difficult to unambiguously state the trade-offs resulting from biodiversity impacts for local communities because members of these communities probably depend on, and benefit from many components and attributes of biodiversity. To the extent that intensive management negatively affects key wildlife populations or any of the functional attributes noted above, local communities will also suffer. On the other hand, community members would benefit if the mammal species that they hunt increase in abundance after logging. In addition, if intensive management decreases the probability of forest conversion, local communities should benefit because the components and attributes of biodiversity will be more complete than if the forest is cleared for other uses.

Local municipalities, national governments, and the global conservation community receive fewer of the direct benefits of biodiversity than local communities, but they have as much to lose if intensive silviculture has negative impacts. In general, their losses have more to do with their personal values than with any direct negative impact on their livelihoods, especially over the short-term. Nevertheless, the local

extirpation species (which may be an inevitable consequence of timber management) and negative consequences described above for loggers constitute costs especially from the perspective of the conservation community. Other negative consequences of biodiversity losses for these stakeholders are difficult to predict, although a recent study found that changes in species composition due to non-random extinction (e.g., due to over-harvested timber species) will alter carbon sequestration potential because of species differences in growth, survival, and wood densities (Bunker et al. 2005).

Management impacts on carbon sequestration

I used the SYMFOR model (Chapter 2) to compare changes in total carbon pools and fluxes in response to each treatment over a 60-year simulation period. Aboveground tree (≥ 10 cm dbh) biomass estimates relied on allometric equations calibrated for tropical moist forests by Chave et al. (2005). To estimate the other aboveground biomass components (e.g., small trees, shrubs, lianas, etc.) and belowground biomass I used reported values of the proportion of total aboveground biomass (TAGB) each of these components comprises in neotropical forests (Table 3-2). Because the large tree (≥ 10 cm dbh) component usually comprises 75%-85% of TAGB (Table 3-2), I assumed that large trees comprise 80% of TAGB in La Chonta. Although most assessments report that lianas only comprise 5% of TAGB, I chose the 14% value of Gerwing and Farias (2000) because La Chonta's liana density is very high (Alvira et al. 2004). Similarly, because approximately 30% of La Chonta comprises gaps and low stature forest (Chapter 1), I assumed that the understory component of TAGB would be slightly higher than the 5% value commonly reported for neotropical forests (Table 3-2). Although belowground biomass (BGB) estimates vary tremendously with soil conditions and climate (Brown 1997), I assumed that BGB would equal 20% of TAGB based on a recent assessment for

the Amazon (Houghton 2005). Finally, I assumed that the mass of carbon would be half of the total above- and belowground biomass because the mass of wood is about 50% carbon (Brown 1997, Houghton 2005).

The model's projections indicated that the no logging control retained the most carbon during the 60-year simulation period, but that the impacts of logging and additional silviculture were relatively small (Figure 3-2). Averaged over 60 years, the total carbon stored in living vegetation was 135.5 ± 1.1 Mg C/ha for the control treatment, 121.1 ± 1.4 Mg C/ha for the normal harvest treatment, and 119.9 ± 1.7 Mg C/ha. When the total timber volume harvested (in years 0, 30, and 60) and time-averaged carbon pools are plotted for the three different management treatments (using the production possibilities frontier model) the effect of a unit change in timber production on the carbon pool is revealed (Figure 3-3). As illustrated in Figure 3-3, the incremental increase in timber yields obtained under intensive management resulted in only a 0.13 Mg/ha reduction in carbon stored over 60 years relative to the normal harvest treatment. Thus, compared to the normal harvest treatment, the intensive management treatment appears to offer a better combination of timber production and carbon stocks as described in Figure 3-1b (see arrow between B and D).

To understand the relative trade-offs between carbon flux and timber production among management treatments, it is important to consider the fate of the carbon in the harvested wood and in the dead and dying vegetation resulting from the treatments. Because these issues have been explored in detail elsewhere (e.g., Marland and Marland 2003), I used simplifying assumptions in this analysis. First, I assumed that the carbon in dead and dying vegetation, as well as in waste during timber processing, would be

immediately emitted to the atmosphere. The fate of carbon in harvested timber depends largely on the end uses and their longevities (e.g., durable products such as flooring, lumber, and furniture vs. short-lived products such as particle board and plywood for cement moldings). I assumed that the wood products (mainly doors and construction grade lumber) produced by La Chonta are durable and that the carbon in them would remain sequestered for ~35 years, which corresponds to an annual decay rate of 0.02. Marland and Marland (2003) used a half-life of 40 years for wood products used in home construction and noted that the half-life of wood products can be 100 years or longer. Keller et al. (2004) used an annual decay rate of 0.01, which would correspond to a half-life of ~70 years. Thus, my assumption of 35 years is conservative. I then assumed that only 50% of the aboveground biomass of harvested trees arrives at the mill and that the wood processing efficiency in La Chonta is 40% (regardless of management intensity) based on recent estimates of milling efficiencies in the Brazilian Amazon (Lentini et al. 2005). I calculated net carbon flux during the simulation period for each treatment by totaling the carbon gains (from growth and recruitment) and losses (from damage, waste, silviculture, milling inefficiencies, and decay of long-lived wood products; see Table 3-3).

During the 60-year simulation period, the control treatment plot accumulated 4.6 ± 6.0 Mg C/ha. Although the intensive management treatment harvested or otherwise removed 37 Mg C/ha, it accumulated 28.9 Mg C/ha for a net loss of 8.1 ± 7.1 Mg C/ha without accounting for processing or C stored in wood products. In contrast, the normal harvest treatment harvested or otherwise lost 12.5 Mg C/ha, but only accumulated 22.9 Mg C/ha for a net C loss of 10.4 ± 6.6 Mg C/ha. When the storage of C in wood

products and losses of C from processing and decay of those wood products are considered, the net loss is 7.1 Mg C/ha for the intensive management treatment and 9.8 Mg C/ha for the normal harvest treatment (Table 3-3). Thus, the net flux of carbon to the atmosphere in the simulated intensive management treatment was 27% less than the flux under the normal harvest treatment.

The quantification of trade-offs between timber production and carbon sequestration should also consider carbon accounting methods because different approaches yield different results (Moura Costa 2001), and because it is important to determine what discount rate (if any) to use to value carbon stored in the future. The rationale for discounting carbon sequestered in the future is that early mitigation of greenhouse gas emissions is worth more than later abatement (Fearnside 1999b). If no discounting is applied, then the net carbon accumulated over the 60-year simulation period under the intensive management and normal harvest treatments are similar (see above and Figures 3-3 and 3-4), and obviously less than the carbon accumulated in the no logging scenario. Under any positive discount rate, it could be argued that because the intensive management treatment resulted in the removal or death of more biomass during each cutting cycle than the normal harvest treatment, it has a lower net present accumulation of carbon (*sensu* Boscolo et al. 1997). However, the small additional loss of biomass resulting from intensive management (relative to the normal harvest treatment) was quickly recovered due to faster growth (Figures 3-2). Thus, I found little effect of discounting (using rates of 2% and 6%) on the net carbon fluxes reported above.

Although it seems reasonable to conclude that at the management intensities applied the trade-offs between timber production and carbon sequestration are modest,

several additional factors should be considered. First, while it is not a surprise that carbon storage was greatest in the no-logging control scenario, it is important to emphasize that neither the likelihood of fires occurring nor the damage a fire would inflict was considered in the simulations. In reality, fires frequently escape from pastures or forests being cleared, especially after prolonged drought and/or logging (Martínez and Cordero 2001, Zarin et al. 2005). Second, pressure to convert forests, especially those degraded by poor logging practices, continues to mount as populations grow, and land reform movements justifiably question central government land allocation decisions. Thus, unless forest conversion is avoided, the carbon sequestered under the no-logging control scenario may very well be emitted. Forest conversion may be less likely under intensive management that maximizes future timber revenues than under no logging or normal harvest scenarios. Finally, if achieving STY requires much more intensive management than tested, it also seems reasonable to conclude that the trade-offs between STY and carbon sequestration would be greater than those reported here.

Stakeholder perspectives. To the extent that the carbon emissions from intensive management contribute to climate change, the costs are borne by all of the earth's inhabitants, at least over the long-term. The forecast from climate models of a drier and warmer regional climate (MSDP 2000) should interest and even concern local stakeholders including communities and the forest industry. Local communities and the forest industry, however, may attribute less value to the global significance of carbon stored in their forests than the conservation community because the benefits of the carbon sequestered in their forests are distributed globally.

Over the short-term, there are two mechanisms by which local communities and the forest industry might financially benefit from any management that reduces the net flux of carbon to the atmosphere: increased efficiency and direct payments from third parties. Reducing harvest damage and wood processing waste and using heavy machinery more efficiently not only reduces carbon losses (Pinard and Putz 1996, Pinard and Cropper 2000, Keller et al. 2004), but also reduces financial costs (Holmes et al. 2002). Over the short-term, forest owners, concessionaires, and loggers may be further motivated to minimize carbon losses if they receive third party payments to do so. Although such a mechanism was rejected from the Kyoto protocol, it is analogous to the persuasive argument of Santilli et al.(2005) to pay tropical governments if they can demonstrably reduce deforestation. By extension, if the forest industry can implement management that reduces carbon emissions, they could be compensated financially. A prototypical compensation system for implementing reduced-impact logging was successfully applied in Sabah, Malaysia (Pinard and Putz 1996).

Management impacts on fire susceptibility and intensity

To assess the trade-offs between timber production and fire susceptibility and intensity, I conducted a series of field experiments and observational studies in La Chonta (Chapter 1). Specifically, I quantified the effects of management intensity on fuel loads, fuel dry-down rates, microclimate, and ability of fire to carry in experimental burn plots 3-6 mo, 1 yr, and 3 yr post-treatment. Although I expected fire susceptibility to increase with management intensity, our field experiments revealed that it did not. Instead, I found that La Chonta is extremely fire prone for ~132 days per year without logging and for only 13–14 additional days per year in the normal harvest and intensive management treatments (Figure 3-4, Chapter 1). Inter-seasonal variability was more important than

treatment effects in determining the number of fire prone days. Moreover, the small increase in susceptibility with logging diminished after 1 year (Chapter 1). Finally, although intensive management slightly increased fire susceptibility in the early dry season, this effect disappeared toward the middle of the dry season.

Although I did not directly measure the management impact on fire behavior, it seems reasonable to infer that if a fire were to occur in La Chonta, it would be more intense and have more severe effects in areas under the intensive management treatment than under the normal harvest treatment. This conclusion is based on the generally positive relationship between fuel loads and fire intensity (Cochrane 2003) and also on observations in other tropical forests of more deleterious fire impacts in logged and other disturbed areas than in relatively undisturbed areas (Cochrane and Schulze 1999, Siegert et al. 2001). The greater quantity of fuels, especially 1,000-hr fuels (coarse woody debris ≥ 7.5 cm diameter), in the intensive treatment plot 6–16 mo post-treatment (Figure 3-4) implies that if a fire were to occur, it would burn hotter, produce more harmful smoke due to prolonged smoldering and be harder to extinguish than a fire occurring in the normal harvest treatment plot. Thus, a fire occurring after intensive management would also cause higher tree mortality rates (Kauffman 1991, Siegert et al. 2001, van Nieuwstadt et al. 2001, Cochrane 2003, Barlow and Peres 2004), greater deleterious impacts on interior forest wildlife (Herrera-Flores 2003, Barlow and Peres 2004), and greater emissions of carbon (Nepstad et al. 1999a, Barlow and Peres 2004).

Stakeholder perspectives. The increasing prevalence of fires in the tropics has alarmed all stakeholders because the costs of fires (including those mentioned above) are incurred at the local, regional, and global scale. Locally, even farmers, ranchers, and

community members who use fire to clear and manage their land incur costs when fires conflagrate because out of control fires destroy homes and property. The smoke from fires stalls traffic and impedes commerce in general. The fine particulates from smoldering fires are particularly damaging to human health. Finally, escaped fires destroy standing timber and any investments in management. Thus, local communities and the forest industry bear enormous costs from fires.

Application to other Tropical Forests

To examine how the forest management trade-offs revealed in La Chonta may differ elsewhere, I contrast La Chonta with forests in the eastern Amazon and eastern Borneo where harvest intensities are 2–10 times greater (Uhl and Vieira 1989, Pinard and Putz 1996, Bertault and Sist 1997). Although forests in both these areas are wetter, evergreen, and have more closed canopies than La Chonta, many of the silvicultural challenges are similar (Appanah and Putz 1984, Whitmore 1985, Silva et al. 1995, Schulze 2003). Moreover, the risks and threats facing La Chonta's managers are similar in these and most other tropical forests. Foremost among these threats are: the increasing prevalence of fires in the ever more fragmented landscape matrix (Woods 1989, Cochrane et al. 1999, Nepstad et al. 2001, Siegert et al. 2001, Cochrane and Laurance 2002); new profitable crop varieties (especially soybeans) that can grow on poor soils (Brown et al. 2005, Hecht 2005); the high profitability of cattle ranching (Uhl and Buschbacher 1985); extreme poverty coupled with insecure land tenure (Dove 1993); and, various incentives to clear forests for other uses (Verissimo et al. 1992, Uhl et al. 1997).

Another important disincentive faced by foresters in most tropical forests is the low market prices for tropical timber. The distortion of timber markets by wood harvested

illegally and from legal deforestation also keeps prices low and dissuades enterprises from investing in long term forest management (Ravenal et al. 2004). In the three tropical forest regions considered here, limited government enforcement capacity, corruption, and governmental instability (at least in the case of Bolivia) exacerbate these unfavorable conditions for forest management.

Three factors motivated my choice of these two regions for comparing with La Chonta. First, both regions have received considerable research attention. Second, in all three areas the timber industry is an important economic driver, but has also contributed to forest degradation and conversion through high-grading, which was often the initial step in forest clearing (Uhl et al. 1997). Finally, the previously atypical fires that have caused heavy damage in both regions in recent decades motivated relevant research. Specifically, the synergisms between logging, cattle ranching, and fire described by Uhl and Buschbacher (1985) were further described as a series of positive feedbacks for both the Amazon (Cochrane et al. 1999, Nepstad et al. 2001), and Borneo (Siegert et al. 2001).

Eastern Amazon

Forests in the eastern Amazon are only slightly wetter than La Chonta (~2000 mm/yr of rainfall), but despite a similarly marked dry season, they remain evergreen because the soils are deep and many canopy trees have deep roots (Nepstad et al. 1995). The dominant soils in this region are Oxisols and Ultisols (Uhl and Vieira 1989), which are more weathered and hence less fertile than the soils of La Chonta. Liana densities are high in the eastern Amazon (Vidal et al. 1997, Gerwing 2004), but only about half as dense as in La Chonta. The canopy is usually less disturbed (only a 3% gap fraction, Asner et al. 2004) and taller, on average, than La Chonta, with emergent trees reaching heights of 50 m (e.g., Holmes et al. 2002).

Although tree species richness in La Chonta and the eastern Amazon is similar, management for STY in the latter may be easier to achieve because it will be simpler to market new species as stocks of currently commercial species dwindle. This assertion is based primarily on the proximity of eastern Amazon forests to both domestic and international markets. This assertion is based primarily on the proximity of eastern Amazon forests to both domestic and international markets, which decreases transport costs and increases the likelihood of new species becoming marketable. Whereas in La Chonta only 10–12 species are typically harvested (Alvira et al. 2004, Chapter 1), in the eastern Amazon the estimate is 40–50 species (Verissimo et al. 1992, Barreto et al. 1998, Holmes et al. 2002). Thus, despite the similar problem of high liana densities, loggers in the eastern Amazon generally harvest twice as many stems (i.e., 4–8/ha) and 2–3 times the volumes as their counterparts in La Chonta. In eastern Amazon forests, average timber volumes range from about 25 m³/ha (Holmes et al. 2002) to 50 m³/ha (Uhl and Vieira 1989) compared to only ~12 m³/ha in La Chonta (Chapter 2).

Based on the growing number of producers (ranging from large, vertically integrated companies to communities) that are adopting reduced-impact logging (RIL) practices and seeking FSC certification, it is evident that the concept of managing forests in the eastern Amazon for STY is gaining traction (Pokornoy et al. 2005). One of the many factors driving this trend is the belief that preventing damage to FCTs and minimizing soil and canopy disturbances will facilitate the achievement of STY (Holmes et al. 2002). Although interest in RIL and certification have helped reduce the frequency of unplanned, destructive logging, evidence to date suggests that additional silvicultural treatments will be necessary to achieve STY unless new species are harvested in place of

those initially harvested. For example, Schulze (2003) found that some of the most valuable species currently harvested either have inadequate regeneration or grow too slowly (or both) to be managed for sustained yields at the current cutting cycle of 25 years. Likewise, projections of a SYMFOR model implemented for eastern Amazon forests concluded that starting in the second cutting cycle, it will be necessary to harvest faster growing tree species with less dense wood to secure STY (Phillips et al. 2004b).

Faced with the potential local extirpation of the currently most valuable tree species in the eastern Amazon (e.g., *Swietenia macrophylla* and *Tabebuia serratifolia*), forest managers will have to weigh the costs and benefits of silvicultural treatments aimed at securing their regeneration (Schulze et al. 2005) or managing for different species. In La Chonta, managers have little choice because of limited market access, whereas in the eastern Amazon, managers do have a choice because of access to various markets that will accept previously unknown species. Their choice will affect the magnitude of the trade-offs among timber production, biodiversity conservation, carbon sequestration, and fire susceptibility and intensity.

The direct effects of logging on biodiversity in the eastern Amazon may be greater than those observed in La Chonta due to the more dramatic impact of logging on forest microclimate. In general, studies on the impacts of logging find a positive correlation between logging intensity and impact on diversity and richness (Putz et al. 2001). Kalif et al. (2001), for example, found that although logging did not alter ant species richness, it shifted the relative abundances of species more in plots that suffered extensive damage from conventional logging than in plots logged with RIL. Azevedo-Ramos et al.

(2005), however, note that studies that correlate changes in populations to environmental changes that result from logging are still needed.

Perhaps the more important difference between eastern Amazon forests and La Chonta is the higher proportion of timber species in the former that are shade-tolerant and animal-dispersed. Thin-barked species with inadequate regeneration, narrow geographical ranges, and dependence on animal dispersers that are preferentially hunted, may be particularly susceptible to local extirpation (Martini et al. 1994). Although these differences are important, the consensus from studies across the tropics is that the indirect effects of logging—especially hunting (Robinson and Bennett 2000) and fire (Laurance 2003, Barlow and Peres 2004)—pose far more ominous threats to biodiversity than the direct effects of logging itself (Putz et al. 2001).

The trade-offs between timber production and carbon sequestration in the eastern Amazon are as challenging to elucidate as in La Chonta. If factors beyond the harvest operations are ignored, it seems reasonable to conclude that the trade-offs in eastern Amazon timber operations (that are similar in scale and sophistication to La Chonta) would be somewhat greater because of the greater timber volumes harvested. The difference in the magnitude of the trade-offs would depend on the intensity of silviculture required to secure regeneration of the most valuable timber species and also on the harvesting system. In simulations of the effects of reduced-impact logging (RIL) and conventional logging (CL) on carbon stocks and fluxes in central Pará, Keller et al. (2004) found that RIL would save about 7 Mg C/ha over 30 years and 13 Mg C/ha over 200 years compared to CL.

Most forests in the eastern Amazon were long considered fire resistant because evergreen canopies keep surface fuels too moist to ignite except during prolonged El Niño associated droughts (Nepstad et al. 1995, Cochrane et al. 1999). Logging renders these forests susceptible to fire because of rapid desiccation of surface fuels once the canopy is opened (Uhl and Vieira 1989, Kauffman and Uhl 1990). Reduced-impact logging mitigates this problem to some extent, but unfortunately, conventional logging practices are still common in the Amazon (Holdsworth and Uhl 1997). The fragmentation caused by land use change (Laurance et al. 2001) and increased access from government road paving programs makes ignition sources plentiful (Nepstad et al. 2001), and has dramatically increased the flammability of much of the Amazon Basin. For example, Cochrane and Laurance (2002) estimated that 13% of the remaining forest in the Amazon is now susceptible to fire.

The more dramatic biophysical impacts of logging in the eastern Amazon (vs. La Chonta) suggest that the trade-offs between timber production and fire susceptibility and intensity are also greater. Considering that selective logging continues to expand in the eastern Amazon and the region is increasingly fragmented (Asner et al. 2005) fire frequencies and intensities will most likely increase. The more frequent and stronger droughts forecast for the region by climate change models (Timmerman et al. 1999) will further increase fire susceptibility. Given that low intensity, surface fires can kill as many 36% of the mid- to upper-canopy trees, which would in turn commit approximately 21 Mg/ha of carbon to the atmosphere (Haugaasen et al. 2003), it is especially critical to implement and enforce fire prevention and control strategies.

Southeast Asian dipterocarp forests

Southeast Asian forests, including those in eastern Borneo, were recognized long ago as being well suited for natural forest management (e.g., Wyatt-Smith 1959). These forests receive the most rainfall of the sites mentioned here (e.g., ~2,700 mm/yr, Pinard and Putz 1996), but have the most challenging terrain with steep slopes ($>20^\circ$) often comprising 75% of management units (Pinard and Putz 1996). But, a single family of tall, well-formed trees—the Dipterocarpaceae—dominates these forests. Forest canopies average 45 m in height and 70 m emergent trees are not uncommon (Pinard and Putz 1996). The dominance of dipterocarps greatly facilitates management for STY because they are massive, wind-dispersed, usually abundant in small size classes, and have desirable wood qualities. Typical harvest volumes range from 80–100 m³/ha (Curran et al. 1999).

Theoretically, STY should be achievable if trained and carefully supervised crews apply reduced-impact logging (Pinard and Putz 1996), and yields are strictly controlled (Sist et al. 1998), at least according to model projections (e.g., Huth and Ditzer 2001, Phillips et al. 2003). At this point, however, most of the forests of this region have been degraded by poor logging practices, converted for agriculture, or damaged by fire (Slik et al. 2002) to the extent that recruitment failures of dipterocarps might eventually doom the timber industry and dramatically change the structure and composition of these forests (Curran et al. 1999).

Although the direct negative effects of logging on biodiversity in Borneo are reportedly smaller than the indirect negative effects (Meijaard et al. 2004), the larger volumes harvested and high levels of damage suggests that the trade-offs between timber production and biodiversity are likely to be greater than noted above for the eastern

Amazon and La Chonta. As Meijaard et al. (2004) note, many species appear to depend on moist understory conditions and connectivity between forest patches. Other evidence from West Kalimantan indicates that the synergistic effects of logging and El Niño related droughts are disrupting the mast fruiting behavior of dipterocarps enough that recruitment failure for this important family has been underway since 1991 (Curran et al. 1999). It is unclear whether the timber industry will be able to address this problem by shifting its harvest to mid-size trees and non-dipterocarps to enable dipterocarp populations to recover.

The high volumes of harvestable timber dipterocarp forests means that the trade-offs between timber production and carbon sequestration are quite high, at least when compared to a no logging scenario (Boscolo et al. 1997). Boscolo et al. (1997) found that both carbon sequestration and biodiversity (measured as the Shannon-Wiener index) are maximized in protected forests. Under a management regime that maximizes timber revenues, carbon storage was 21% lower than when it is not logged (Boscolo and Buongiorno 1997). Similarly, using a projection model calibrated for forests in Sabah, Pinard and Cropper (2000) found that, after selective logging, ecosystem carbon storage declined to only 45% of the pre-logging level (213 Mg/ha) and required 120 years to recover. When simulated damage was reduced by use of RIL methods, mean carbon storage was 36 Mg/ha greater over 60 years than in conventionally logged areas (Pinard and Cropper 2000).

Although the trade-offs between timber production and carbon sequestration could be minimized and STY could be achieved by the careful application of RIL with strict yield regulation, apparently the opportunity or other costs are high enough such that the

adoption of this management strategy has been slow (Healey et al. 2000). The ‘other’ costs include fire prevention and controlling access to the managed forest.

The problem of increasing fire frequency and severity in eastern Borneo has followed a parallel trajectory to that observed in the Amazon. Logged forests are more susceptible to fire and suffer more intense fires when they occur (Siegert et al. 2001, van Nieuwstadt et al. 2001). Most tree species are poorly adapted to fire and fire related-mortality is high (Woods 1989, Curran et al. 1999); in addition, recovery from fire is extremely slow (Slik et al. 2002). Thus, the positive feedbacks described for the Amazon also occur in Borneo (Siegert et al. 2001) and few forests have been unaffected by fires. For example, 90% of Kutai National Park burned in the 1998 fires in East Kalimantan (cf. Slik et al. 2002).

Summary of Trade-offs in Three Tropical Forests

Several key points emerge from the assessment of trade-offs in La Chonta and the comparisons with the eastern Amazon and Borneo. First timber production, carbon sequestration, and biodiversity conservation are not mutually exclusive goals these regions, at least not when only the direct effects of silviculture are considered. Second, timber production objectives obviously do compete with the globally important goals of carbon sequestration and biodiversity conservation, but the trade-offs are neither linear (in the case of carbon sequestration) nor always clear and consistent (in the case of biodiversity). The intensive silviculture apparently required to achieve STY may initially increase the magnitude of these trade-offs, but if fire, hunting, and other indirect effects of timber production are prevented, model projections suggest that these trade-offs quickly diminish as the forest recovers.

The biodiversity trade-offs are especially difficult to elucidate because they depend on the particular components and attributes studied (Noss 1990, Putz et al. 2001), the temporal and spatial scale of assessments (Hill and Hamer 2004), and the fate of the managed forest (Dunn 2004). Biodiversity impacts at higher levels (e.g., ecosystem to landscape) depend greatly on the surroundings (Hill and Hamer 2004). Impacts at lower levels (community to genetic) vary with the taxa studied, the relative importance of direct vs. indirect effects of logging, and the spatial and temporal scale of the study (Hill and Hamer 2004). The fate of the forest after logging is important because the diversity of forest-interior birds, mammals, and butterflies are more detrimentally affected by forest conversion than by direct logging effects per se (Dunn 2004, Meijaard et al. 2004).

Finally, because forest conversion is often accomplished with fire (or is a consequence of fire), and because logged forests are especially prone to destructive fires, the risk of fire is perhaps the most appropriate factor to consider when assessing trade-offs. This perspective seems especially important considering that El Niño events are projected to become stronger and more frequent as a result of global warming (Timmerman et al. 1999), and that the regions considered here are expected to become drier and warmer (MSDP 2000, cf. Barlow and Peres 2004). The warmer, drier climate coupled with an abundance of ignition sources in the fragmented landscape matrix surrounding most production forests have changed ecosystems in which fires were historically rare into fire-prone systems whose principal biota are not fire-adapted. Thus, because fire is now such a dominant threat to tropical forests, vigilant and coordinated fire prevention and management strategies are necessary (though not necessarily

sufficient) to avoid forest conversion where forestry is practiced (Figure 3-5, Chapter 1, Barlow and Peres 2004).

Policy Options to Minimize Trade-offs

Various policy options have been promulgated to minimize or eliminate the risk of forest conversion (Table 3-4, Ferraro and Simpson 2002). Direct options include purchase and protection of forestland. Indirect options include removal of disincentives (e.g., removal of subsidies for cattle ranching in forest lands), promotion of STY through timber certification, training, and research, and payments for environmental services (PES).

The PES option has received substantial attention in recent years because it tries to take account of the stakeholders to whom the benefits of forest management objectives accrue (Balmford and Whitten 2003). Another appeal of PES for policymakers is its potential as a mechanism to reduce poverty (Wunder 2001). The logic of PES is based on the accepted notion that carbon storage, other ecosystem services, and biodiversity are global values. Since rich countries benefit from the biodiversity, ecosystem services, and other values of tropical forests, they should pay to maintain them (Balmford and Whitten 2003).

The PES concept is especially compelling when the consequences of not controlling fire in tropical forests are considered. In addition to the loss of valuable timber, fires in tropical forests cause other deleterious effects described above. Although more research on the impacts of fires on biodiversity and the potential consequences for achieving STY are needed, the Brazilian Amazon studies cited above report strong negative impacts on forest interior birds and mammals as well as high mortality rates for

canopy trees. Thus, it would be interesting if the PES concept could be integrated with fire prevention and control strategies.

Conclusions

The main conclusion of this paper is that the trade-offs resulting from intensive silviculture to secure STY pale in comparison to deforestation, which continues unabated at a rapid rate (Archard et al. 2002). If maintenance of productive forest (for both timber and carbon) with a full complement of biodiversity is the goal, then fire (and not silviculture) is the menace. Indeed, to the extent that silvicultural treatments can help achieve STY, and hence increase the forest's NPV, they should be applied without fear of excessively diminishing other forest values. I presented three lines of evidence from three tropical forests to support this conclusion. First, timber production and carbon sequestration trade-offs are generally modest and, in most cases, can be mitigated if management includes forest protection. Second, in most cases, timber production is compatible with biodiversity conservation if simple measures are implemented to mitigate the direct deleterious effects of silviculture, and precautions are taken to minimize the more perilous indirect effects (Meijaard et al. 2004).

Finally, although logging and additional silvicultural treatments increase the susceptibility to fire of evergreen tropical forests, other landscape scale factors are more worrisome. The especially high susceptibility of fragmented forests to fire, hunting, and other drivers of land use change should motivate policy makers to protect the remaining large tracts of relatively undisturbed forest (Peres 2005) while simultaneously implementing strategies to prevent and control fires .

The consequences of not controlling fire are profound and only slowly becoming clear. Considering the growing area of tropical forests that are situated at the interface of

savannas, the inability to control fires coupled with the greater potential for severe fires (due to synergisms with logging) will degrade tropical forests. As fires recur (Cochrane and Schulze 1999), they may ultimately shift tropical forest ecosystems from their current relatively stable state to a new state characterized by degraded woodlands and scrub- and savanna-like vegetation (Uhl and Nepstad 2000). In drier forests like La Chonta, this shift is already visible in the surrounding matrix of pastures, palm-dominated savannas, and sparse woodlands. Under most global climate change scenarios, the potential fate of La Chonta could be a harbinger for forests in other parts of the tropics (Uhl and Nepstad 2000).

An important lesson from La Chonta and the other forests considered here is that while the deleterious effects of intensive management to achieve STY should be mitigated, increased attention must be paid to the prevention of fires, hunting, illegal logging, and efforts to convert forest lands to other uses. In that regard, FSC certification of timber and NTFPs, together with PES schemes, should require verifiable fire management plans that are effectively implemented. Development and implementation of such plans might be accomplished most efficiently if it is widely recognized that the benefits of such efforts accrue to both forest owners and the global community.

Table 3-1. Some silvicultural impacts on different attributes of the community component of biodiversity in La Chonta.

Attribute	Treatment	Effects	Source
Structure: liana density and cover	Pre-harvest liana-cutting	Decreased liana basal area and cover 8 months post-treatment	Alvira et al. 2004
Structure: liana density and cover	Pre-harvest liana-cutting	Densities and cover of liana were no different 3 years post-treatment	Terceros unpublished
Structure / Function: liana / community interactions	Liana cutting	<ul style="list-style-type: none"> • No change in soil-water availability • Increased canopy openness by 4% after 26 months • Increased height growth and leaf production of tree seedlings 	Perez-Salicrup 2001 (Note: this study took place in a vine-dense forest outside of La Chonta)
Composition	Logging and/or fire	<ul style="list-style-type: none"> • No affect on tree seedling survival • Species richness higher in disturbed areas • Abundance of frugivores and omnivores higher in disturbed areas • Canopy insectivores and near-ground omnivores most abundant in intact areas • Generalists more abundant in disturbed areas 	Woltman 2003
Structure: canopy cover and woody debris; Composition: small mammal and herpetofauna abundance and richness	Logging and fire	<ul style="list-style-type: none"> • Canopy cover 24% lower in disturbed areas • Woody debris cover 2.6 times greater • Small mammal abundance 43% higher and richness 70% higher • No change in herpetofauna abundance • Herpetofauna richness higher in disturbed • Terrestrial invertebrate abundance (from pitfall traps) higher in undisturbed areas • Patterns above varied by species 	Fredericksen and Fredericksen 2002

Table 3-1. Continued

Attribute	Treatment	Effects	Source
Composition	Logging	<ul style="list-style-type: none"> • Abundance as measured by captures varied by season (most in early dry season) • Increased abundance and richness in felling gaps 1 to 2 years post-harvest • Generalists and disturbance-adapted species were more abundant in felling gaps • Interior forest species were equally abundant in gaps and forest interior 	Flores et al. 2001
Composition	Logging	<ul style="list-style-type: none"> • Impacts (+ or -) on mammal and bird abundance and richness depended on body size as well as temporal and spatial scales of sampling • Mammals of intermediate body size were apparently more affected by season than by management intensity. 	Quiroga and Herrera-Flores 2003
Structure	Logging	Relatively small impacts with direction of impact being species dependent	Herrera-Flores 2003
Structure	Logging	<ul style="list-style-type: none"> • 40–45% of forest disturbed by logging (and previous natural disturbances) • Mean felling gap size was 224 m² (36–1091) 	Ohlson-Kiehn et al. 2003
Structure	Logging	Roads, skid trails and log landings disturbed 25% of forest ground area; felling gaps disturbed another 25% of forest area	(Jackson et al. 2002)

Note: See Noss (1990) for a description of the components and attributes of biodiversity.

Table 3-2. Factors used to estimate aboveground biomass components based on the proportion of total aboveground biomass (TAGB) they comprise according to several recent studies.

Source	Location	Proportion of TAGB (%)			BGB (%) ^b
		Trees ≥10 cm	<10 cm ^a	Lianas	
Brown (1997)	Neotropical average		3–30		4–230
Gerwing and Farias (2000)	Eastern Amazon			14	
Nascimento and Laurance (2002) ^c	Central Amazon	92	5	2	
Jaramillo et al.(2003) ^d	Mexico dry forest	70–93	8–22	8	7.2–11.5
Dewalt and Chave (2004)	4 neotropical forests	85	4.2	4.7	
Keller et al. (2001)	Eastern Amazon	79	14	6	17
Houghton et al. (2001) ^e	Neotropics				20.5
Houghton (2005)	Amazon Basin				20
My study ^f	Bolivia	80	6	14	20

^a Includes trees <10 cm dbh, except Keller et al. 2001 (<15 cm dbh) and Jaramillo et al. 2003 (<7.5 cm dbh for dry forests). The value for Brown 1997 includes lianas, shrubs, herbs, and seedlings.

^b BGB = belowground biomass estimated as a percentage of TAGB

^c Although this study included necromass in their estimates of TAGB, the values shown here only include live biomass components to enable comparison with the other values, which only comprise live biomass.

^d Ranges are for the floodplain and dry forest means; the understory component comprised a greater proportion of TAGB in the dry forest and BGB was also greater in the dry forest.

^e The estimate is the mean of 14 sites across tropical America including the Caribbean; range: 13–34%.

^f I used these values to calculate TAGB and BGB from the aboveground biomass estimates output by SYMFOR. I then used the estimates of TAGB and BGB to estimate total carbon in Figures 3-2 and 3-3.

Table 3-3. Simulated management treatment effects on carbon flux over 60 years in La Chonta.

Source of C storage or loss	Control	Normal harvest ^a		Intensive management ^a			
	Total	Yr-0	Yr-30	Total	Yr-0	Yr-30	Total
Harvested trees ^b		-4.0	-1.3	-5.3	-5.6	-2.7	-8.3
Wood products after processing ^c		1.6	0.5	2.1	2.3	1.1	3.3
Wood products @ 60 years ^d		0.5	0.2	0.6	0.7	0.3	1.0
C emitted from products over 60 years		-1.1	-0.4	-1.5	-1.6	-0.7	-2.3
Damage, waste, and silviculture		-13.7	-4.7	-18.4	-18.2	-10.6	-28.7
Milling		-2.4	-0.8	-3.2	-3.4	-1.6	-5.0
Total C loss	2.7	17.2	5.8	23.0	23.1	12.9	36.0
Total C gain	7.3	3.2	10.0	13.2	13.3	15.6	28.9
Net change in C over 60 years	4.6			-9.8			-7.1

^a Control treatment = no logging; normal harvest treatment = timber harvesting only at years 0 and 30; intensive management treatment = harvesting and additional silviculture at years 0 and 30.

^b Values equal 50% of estimated aboveground biomass (i.e., amount arriving at mill) × 50% carbon content.

^c Refers to long-lived wood products (e.g., doors) and assumes a mill efficiency of 40%.

^d Assumes an instantaneous decay rate of 0.02, which implies a half-life of ~35 years.

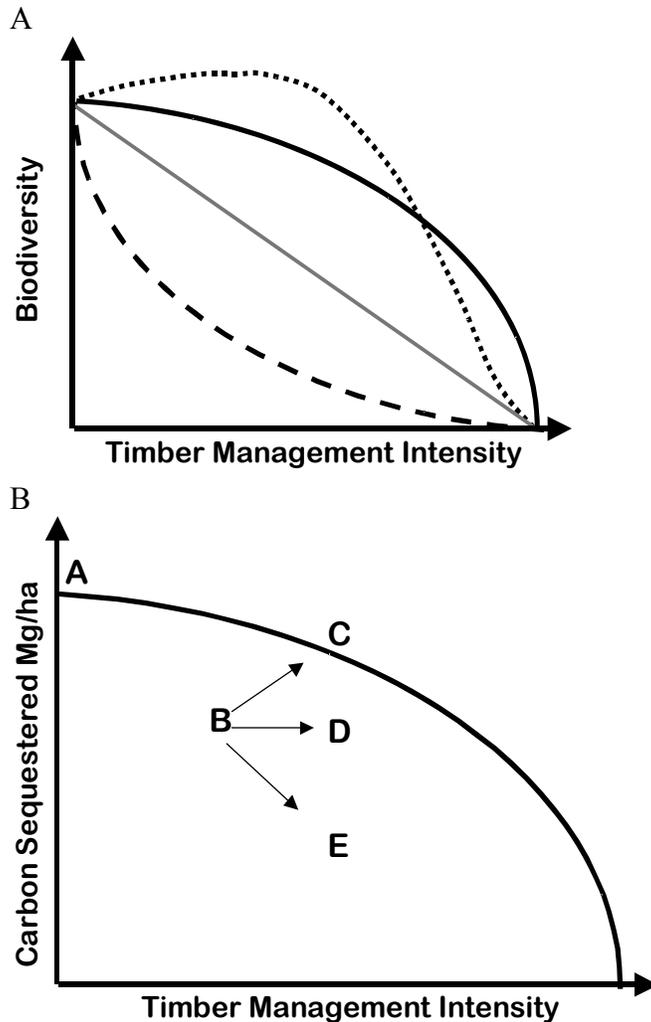


Figure 3-1. Production possibilities frontiers showing several types of trade-offs resulting from joint production of timber, biodiversity, and carbon. A) Four kinds of trade-offs are imaginable for the joint production of timber and biodiversity: incompatible: dashed curve; competing: solid dark curve; complementary: dotted curve; and an exact trade-off: thin straight line. B) A convex curve indicates the biophysical production limits (i.e., frontier) for both timber yields and carbon stocks. Theoretically, all points along and below the frontier are joint production possibilities. The letters indicate hypothesized production sets resulting from three different management treatments of increasing intensity applied in La Chonta: A: control; B: normal harvest treatment; and C–E: intensive management treatment. A movement toward the frontier (e.g., B to C or D) is generally interpreted as an improvement in management outcomes (i.e., higher level of joint production). Movements along the curve could also be viewed as improvements depending on stakeholder perspective and the distribution of benefits and costs. In contrast, any movement away from the frontier (e.g., B to E or toward either axis) implies a greater trade-off. Figure 3-1b adapted from Rapp (2004).

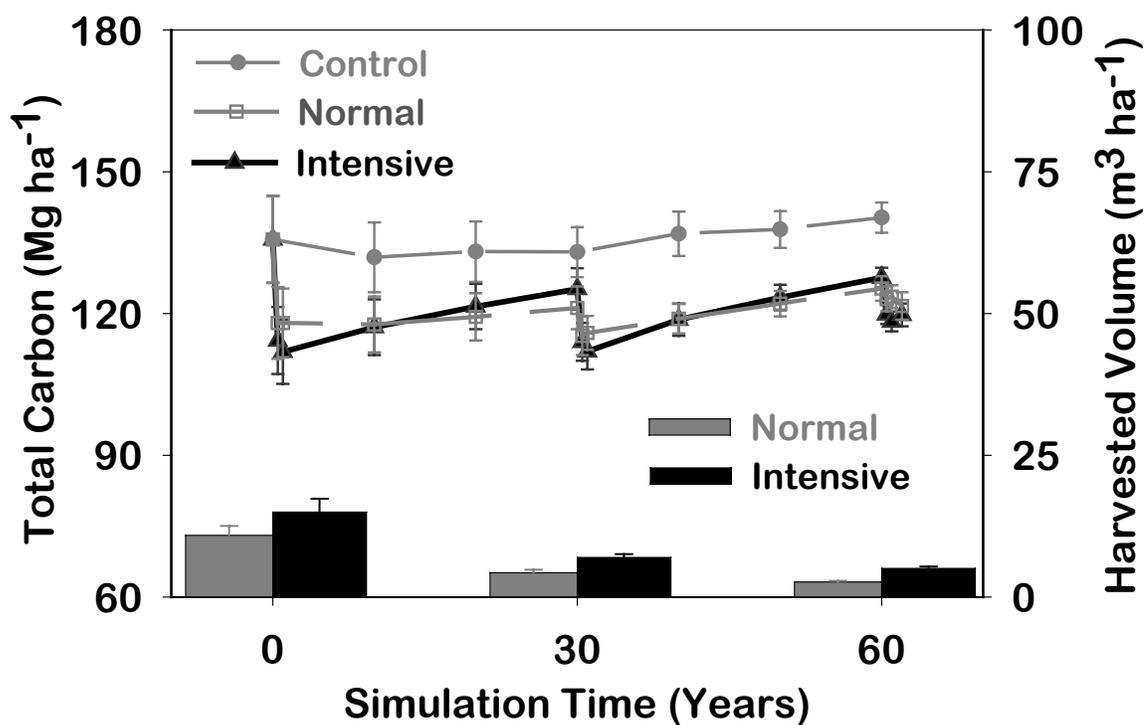


Figure 3-2. Timber volumes obtained and change in total carbon pools in response to three different management treatments applied in La Chonta. The timber volumes were obtained in 3 simulated harvests at years 0, 30 and 60 (normal harvest = gray bar; intensive management treatment = black bar). Total carbon (lines) was estimated from aboveground biomass (see Table 3-2). Error bars are standard errors of the mean resulting from plot differences (n=15).

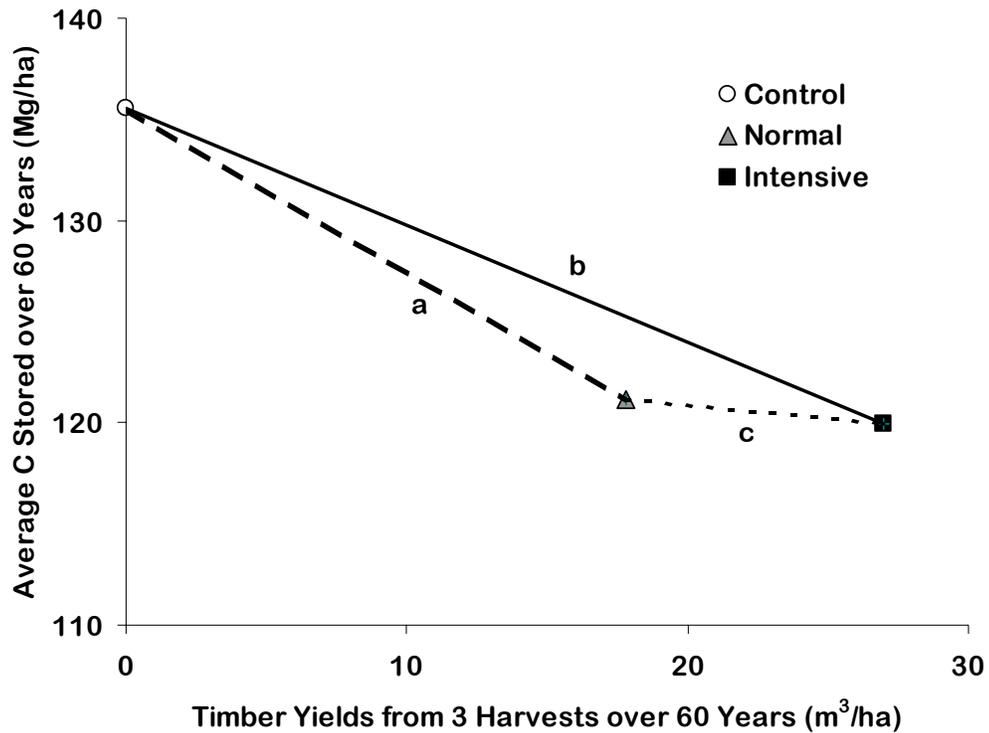


Figure 3-3. Production possibilities for timber and carbon based on forest management options in La Chonta simulated with SYMFOR for 60 years. The data points are cumulative timber yield (m³/ha) over 3 cutting cycles and time-averaged carbon pools (Mg/ha) for the no logging control (open circle), normal harvest (gray triangle) and intensive management (dark square) treatments (see Chapter 2 for details). The slopes of the lines (a, b, and c) connecting the points indicate the relative magnitude of the trade-offs between pairs of management treatments. The slopes are: a: -0.81 , b: -0.58 , and c: -0.13 .

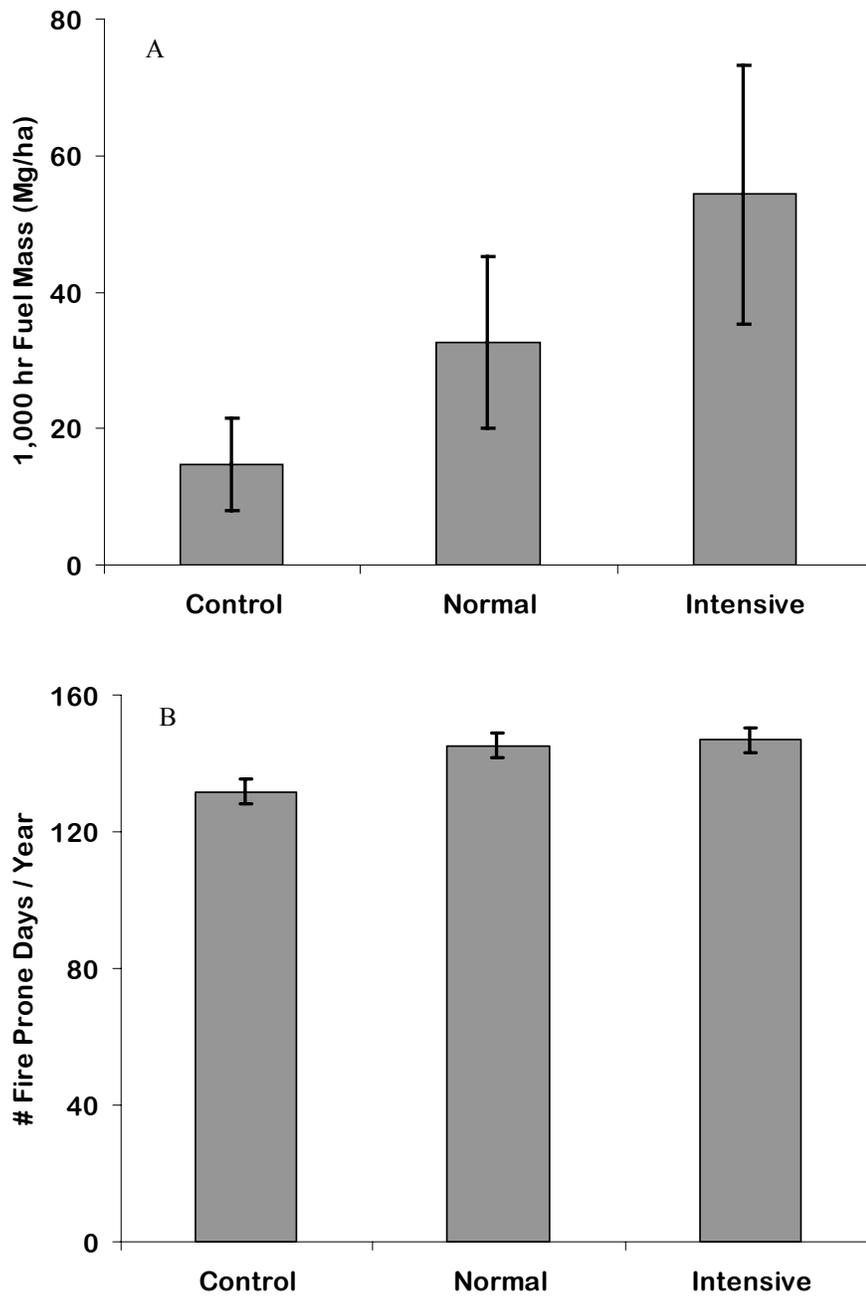
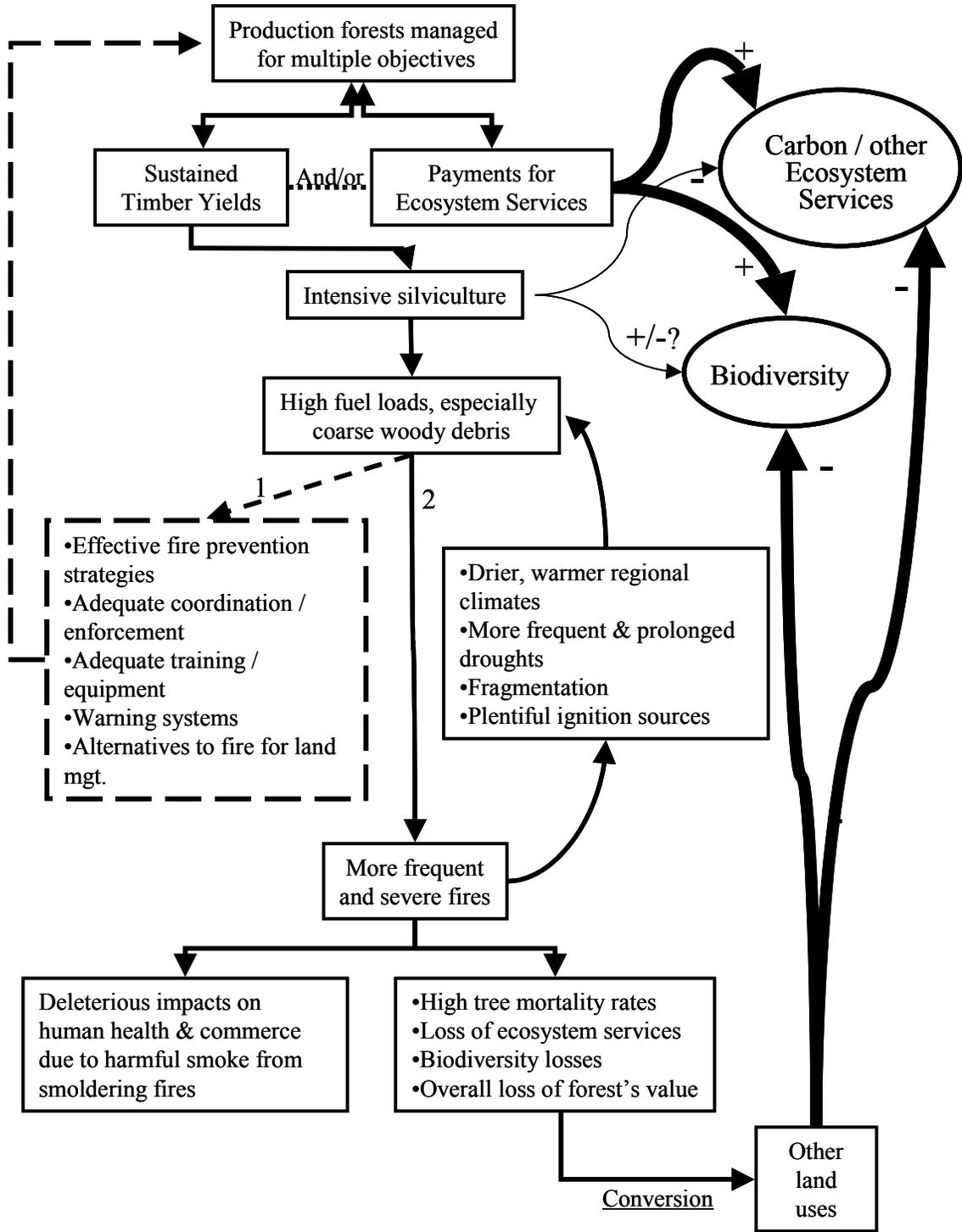


Figure 3-4. Management treatment impacts on 1,000-h fuel loads and number of fire prone days in La Chonta. A) The means for 1,000-h fuel loads (Mg/ha) are for coarse woody debris (dbh > 7.5 cm) sound and intermediate decay classes, and are based on censuses conducted 6 and 15 months post-treatment. Error bars are standard errors of the means. See Chapter 1 for measurement methods and Table 1-4 for sample sizes. B) The number of fire prone days per year is taken from Chapter 1. Error bars are standard errors of the means calculated using 5 years of daily rainfall records.

Figure 3-5. A conceptual model showing two extreme pathways and corresponding trade-offs resulting from a strategy to conserve tropical production forests through sustainable timber production (STY) with or without payments for ecosystem services (PES). Achieving STY generally requires intensive silviculture because otherwise most commercial timber species grow too slowly and/or lack adequate regeneration to provide sustained yields within reasonable cutting cycles. The positive correlation between silvicultural intensity and wildfire, along with landscape and climatic factors that increase fire susceptibility make this strategy for forest conservation risky. Without fire prevention (pathway 2, solid arrows) the trade-offs of this strategy for carbon and other ecosystem services and biodiversity are large (thick arrows, negative symbols). Fire prevention (pathway 1, broken arrows) is essential to mitigate the risks and associated trade-offs (thin arrows) of this strategy.



APPENDIX A
VARIABLES AND PARAMETERS USED IN CHAPTER 2

Table A-1. Variables, parameters, and the equations or tables in which they are used in the SYMFOR model described in Chapter 2.

Variable / Function	Purpose / Description	Estimated parameters	Equation or Table
C_t	Calculated competition index of each tree		Eq. 2-1
d	Distance (m) between two trees		Eq. 2-1
\hat{C}_t	Estimated competition index	a_0 and a_1	Eq. 2-2
C	Diameter-independent competition index		Eq. 2-3
D	Diameter at breast height or 1.3 m (dbh)		Eqs. 2-1, 2-2, 2-3, 2-6, 2-8, 2-10, 2-13, 2-14
I	Diameter increment (cm/yr)	p_0 - p_5	Eq. 2-3
L	Liana infestation class; L_0 =liana-free; L_1 =liana-infested		Eq. 2-3
I_{95}	Diameter increment of trees with $D > D_{95}$	p_6 and p_7	Eq. 2-4
F	Annual probability of recruitment	i_1 and i_2	Eq. 2-5
I_m	Mean diameter increment rate		Eq. 2-5
M_p	Linear predictor of the logistic regression for 'natural' mortality	m_{15} , m_2 - m_4	Eq. 2-6
M	Annual probability of mortality		Eq. 2-7
M'	Annual probability of mortality of trees with $D > D_{95}$		Eq. 2-8
m_5^*	Maximum mortality probability; varied during testing and sensitivity analysis from m_{95} to 1		Eq. 2-8
m_{95}	Probability of mortality of trees with $D = D_{95}$	m_6 and m_7	Eq. 2-8, Eq. 2-9
D_{95}	95 th percentile of the dbh distribution		Eq. 2-8
D_{max}	Maximum diameter of trees in each species group		Eq. 2-8
m_d^*	Parameter used to adjust mortality in Eqs. 2-7 and 2-8 downward due to damage-related mortality ($= P_f \cdot P_d$)		
ω	Ratio of the wood density of the colonizing pioneers to the wood density of each of the other species groups,	Table 2-11	

Table A-1. Continued

Variable / Function	Purpose / Description	Estimated parameters	Equation or Table
H	Total tree height (m)	H_{max}, h_1, h_2	Eq. 2-10, Eq. 2-12, Eq. 2-13
V	Tree volume (m ³)		Eq. 2-11
G	Basal area (m ²)		Eq. 2-11
c_p	Crown-point (estimate of merchantable height)		Eq. 2-11
f	Form factor for estimating volume		Eq. 2-11
a	Ratio of merchantable height to total tree height		Eq. 2-12
B	Tree biomass		Eq. 2-13
ρ	Species group specific wood density	Table 2-11	Eq. 2-13, Eq. 2-14
K_d	Biomass decay function		Eq. 2-14
N	Number of trees		
N_l	Proportion of trees that are liana-infested		
P_L	Probability that recruits will become liana infested based on species group and neighborhood liana infestation class	Table 2-6	
S	Sensitivity; calculated for sensitivity analysis		Eq. 2-16
SG	Ecological species group		Table 2-1
E_s^*	Scarify effect parameter; increases or decreases recruitment rate (Eq. 2-5) in scarified gaps depending on species group	Table 2-14	
L_c^*	Annual probability a liana-free tree will become liana infested	Appendix B	
P_f^*	Probability a tree will die falling (vs. standing)		Table 2-15
P_d^*	Probability a falling tree will kill a neighbor		Table 2-15
D_f^*	Diameter below which trees die standing		Table 2-15
T_i^*	Years required for a tree to recruit (i.e., reach 10 cm dbh) in forest areas cleared of all vegetation (e.g., skid trail or scarified area)	Table 2-8	Table 2-15

APPENDIX B
ANNUALLY UPDATING THE LIANA CLASS OF EXISTING TREES IN SYMFOR

I calibrated the function that updates the liana class of each tree based on the assumption that the proportion of liana-infested trees will be relatively constant over time. I assumed that the proportion of large trees (dbh ≥ 40 cm) with lianas (70%) represented the equilibrium level of liana infestation, which, in effect, is an asymptotic ceiling for the proportion of liana-infested adult trees in the stand (L_a). The proportion of recruits (i.e., dbh = 10–15 cm) with lianas (38%) represented the lower limit (L_j). I then assumed that, over time, liana infestation would increase linearly from the lower limit (L_j) to the upper limit (L_a) over a 75-year period. This last assumption implies an annual growth rate of 4 mm; the mean growth rate in La Chonta for trees > 10 cm dbh is 3.8 mm/yr (IBIF, unpublished data).

To estimate the parameter that determines the rate at which liana infestation occurs in the stand over time, I tried to account for the higher mortality observed in liana-infested trees by using Equation B-1:

$$\frac{dL}{dt} = i(1 - L) - d \cdot L \quad , \quad \text{[B-1]}$$

where i is infestation rate, L is the proportion of liana infested individuals, and d is the difference in mortality between liana-infested and liana-free individuals. The integral of this equation yields:

$$t_a - t_j = -(i + d) \cdot \left(\log(i - (i + d) \cdot L_a) - \log(i - (i + d) \cdot L_j) \right) \quad , \quad \text{[B-2]}$$

where L_a is the proportion of liana infested trees > 40 cm dbh, L_j is the proportion of liana infested recruits (with dbh < 15 cm), and $t_a - t_j$ is the average time required for a 10 cm dbh tree to attain 40 cm dbh. I can re-write this equation and solve for L_a to show that $i/(i + d)$ is the asymptotic liana infestation rate:

$$L_a = \frac{i - (i - (i + d) \cdot L_j) \cdot \exp(-(t_a - t_j)/(i + d))}{(i + d)}, \quad [\text{B-3}]$$

When t_a is much larger than t_j (i.e. there is an indefinite amount of time for infestation), I get $i/(i + d)$, as I should; when $t_a = t_j$ (no time for infestation), I get L_j . Because this equation cannot be solved analytically, I solved for i numerically by assuming that $L_a = 0.7$, $L_j = 0.38$, $t_a - t_j = 75$, and $d = 0.02$. The value of d is the mean difference in mortality rates across all species groups and dbh classes (IBIF, unpublished data). I plotted Eq. B-3 in R (Version 1.7.1) and obtained a value of 0.0475 for i .

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BIOGRAPHICAL SKETCH

Geoffrey Michael Blate was born in 1962 in Long Island, New York. His intellectual journey was sparked by conversations and experiences shared with his extended family and high school friends. Toward the end of college at the University of Rochester, where he earned a B.S. in Neuroscience, his journey took an important turn. Rather than pursue medical studies, he earned a master's degree in education from the University of Massachusetts, and then taught middle and high school science for 5 years. His wonder about the natural world and interactions with his students led him to take a field ecology course in Monteverde, Costa Rica, where he became hooked on tropical biology and decided to pursue a master's degree in environmental studies at Yale School of Forestry and Environmental Studies (1991–1994). After graduating from Yale, he worked for 4 years at the Tropical Forest Foundation in Alexandria, VA, where he coordinated and helped develop a research, training, and outreach program to promote better forest management in the Brazilian Amazon. During this time, he met Sujata Sarah Ram, who he married in 1997. The next year, Geoffrey began his doctoral work at the University of Florida. Upon graduation, he plans to teach and to continue conducting research that will contribute to tropical forest conservation.