DEMOGRAPHY AND HARVEST POTENTIAL OF LATIN AMERICAN TIMBER SPECIES: DATA FROM A LARGE, PERMANENT PLOT IN PANAMA

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CONDIT, R., HUBBELL, S.P. & FOSTER, R.B. 1995. Demography and harvest potential of Latin American timber species: Data from a large, permanent plot in Panama. Basic demographic data on valuable timber species in the tropics are seldom known but crucial for sustainable management. With data from a permanent, 50-ha census plot, we examined mortality and growth patterns and simulated timber harvest for a dozen prominent wood-producing species of Latin America. Standing wood volume was high for three of the species - 44 m^3 ha^{-1} in *Hura crepitans*, 25 m^3 ha^{-1} in *Anacardium excelsum*, and 22 m^3 ha^{-1} in *Prioria copaifera* - but the first two lacked advance regeneration in the plot. Annual mortality rates of individual species varied from below 1% y^{-1} to as high as 2-3% y^{-1}. Regressions of instantaneous relative growth rate on stem diameter (dbh) provided lifetime age-size relations, starting at 10 mm dbh, for seven species. Species fell roughly into three groups: one species took 60 years to reach 300 mm dbh at mean growth, four species took 100-150 years (depending on census interval), and two took > 200 years. Projected survivorship from 10 to 300 mm dbh was > 50% in moderate-growth species with low mortality but < 10% in slow-growing species with high mortality. A simulation model was developed in seven species to predict timber yield for 120 years after an initial harvest. Recruitment was not simulated, so the model only addressed the production of residual stems left from the first harvest. In four species, future harvests were so low relative to the initial harvest that sustainable management would not likely be feasible, but in three, the productivity of future harvests was reasonably high. Judging by total wood production after 120 years, each had a different optimum harvest schedule: for *Cordia alliodora*, a 30-year rotation coupled with a 300-mm dbh minimum harvest size led to the largest total wood output;

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for *Calophyllum longifolium*, it was a 60-year rotation and 300-mm limit; and for *Prioria*, a 60-year rotation and 600-mm limit. Variation between species in demography and schedules of sustainable wood production illustrates the need for management schemes that are tailored to individual species.

Key words: Tropical forest demography - models for timber harvest

CONDIT, R., HUBBELL, S.P. & FOSTER, R.B. 1995. Potensi demografi dan potensi penuaian spesies kayu Amerika Latin: Data dari satu plot yang besar dan kekal di Panama. Data demografi yang asas mengenai spesies kayu yang berharga dalam kawasan tropika jarang diketahui tetapi penting untuk pengurusan berkekalan. Kami mengkaji kemortalan dan pola tumbesar dan simulasikan penuaian kayu untuk satu dozen spesies Amerika Latin yang mengeluarkan kayu dengan menggunakan data dari satu plot banci 50 ha yang kekal. Isipadu kayu dirian adalah tinggi untuk tiga dari spesies-spesies tersebut - 44 m^3 ha^{-1} dalam *Hura crepitans*, 25 m^3 ha^{-1} dalam *Anacardium excelsum* dan 22 m^2 ha^{-1} dalam *Prioria copaifera* - tetapi *Hura crepitans* dan *Anacardium excelsum* kekurangan pemulihan pendahuluan di dalam plot. Kadar kemortalan tahunan bagi setiap spesies berbeza-beza dari bawah 1% y^{-1} hingga setinggi 2 - 3%y^{-1}. Regresi kadar tumbesar relatif pada diameter batang (dbh) memberikan hubungan umur-saiz masa hidup, bermula pada 10 mm dbh untuk tujuh spesies. Spesies-spesies dapat dibahagikan secara kasar kepada tiga kumpulan: satu spesies mengambil masa 60 tahun untuk mencapai 300 mm pada dbh tumbesar min, empat spesies mengambil masa 100-150 tahun (bergantung pada selang banci) dan dua spesies mengambil masa > 200 tahun. Kemandirian ramalan dari 10 hingga 300 mm dbh ialah >50% dalam spesies tumbesar-sederhana dengan kemortalan rendah tetapi < 10% dalam spesies lambat tumbuh dengan kemortalan tinggi. Satu model simulasi dibangunkan dalam tujuh spesies untuk meramalkan hasil kayu bagi 120 tahun setelah penuaian pertama. Perekrutan tidak disimulasikan, jadi model ini hanya mengemukakan pengeluaran dahan-dahan baki dari penuaian pertama. Di dalam empat spesies, penuaian-penuaian pada masa depan agak rendah secara relatif berbanding dengan penuaian permulaan di mana pengurusan berkekalan adalah tidak mungkin; tetapi di dalam tiga spesies, produktiviti bagi penuaian di masa hadapan adalah tinggi. Berdasarkan jumlah pengeluaran kayu setelah 120 tahun, setiap spesies mempunyai jadual penuaian optimum yang berbeza: untuk *Cordia alliodora*, putaran 30 tahun disertai dengan 300 mm dbh saiz penuaian minimum memberikan hasil jumlah kayu yang terbesar; bagi *Calophyllum longifolium*, jadualnya merangkumi putaran 60 tahun dan had 300 mm; dan untuk *Prioria*, putaran 60 tahun dan had 600 mm. Perbezaan antara spesies dari segi demografi dan jadual pengeluaran kayu secara berkekalan menunjukkan betapa perlunya skim-skim pengurusan khusus untuk setiap spesies.

Introduction

Extracting goods from tropical forests on a sustainable and economically viable basis demands detailed information on the population dynamics of individual species. Basic demographic parameters of growth and survival are needed to develop precise quantitative models of harvest. Only then can programmes for sustainable harvest be developed and the long term value of the forest resource be assessed (Panayotou & Ashton 1992). Yet for most tree species in tropical forests, even many of the most valuable, adequate data on basic biology are lacking (Hubbell & Foster 1992).

In 1980, a large-scale, permanent census plot was installed in the tropical moist forest on Barro Colorado Island in central Panama with the intention of gathering detailed, basic information on a large number of tropical tree species (Hubbell & Foster 1983, 1992). Complete censuses of the 50-ha plot were completed in 1982, 1985, and 1990, with all stems down to 10 mm in diameter included. The justification for the large size of the plot was that in diverse forests individual species are not common, and a large census area was necessary to gather large sample size for most species (Condit *et al.* 1993a, Condit 1995). The small lower size limit for the census was necessary to gather information on growth and mortality of trees throughout most of their lives. Parallel 50-ha plots have now been established in Peninsular Malaysia (Manokaran *et al.* 1990, Saw *et al.* 1991) and in India (Sukumar *et al.* 1992), with similar goals in mind for very different tropical forests, and additional large plots are underway in Zaire, Cameroon, Sri Lanka, Thailand, Sarawak in Malaysia, the Philippines, Ecuador and Puerto Rico (Zimmerman *et al.* 1994, Condit 1995).

We selected for analysis here a dozen species that occur in the 50-ha plot in Panama and which are known locally as important timber trees. Six of these are among the top 10 in Panama in wood volume harvested, and the remaining are known for high quality timber or as productive plantation species. There is virtually no information available on the abundance and demography of these species in natural forests (except for *Prioria*: Mayo Melendez 1965, Valle 1979, Rovira *et al.* 1987, Linares 1987, 1988, Linares & Martinez 1991). Here we present basic information derived from the 50-ha plot on abundance, size distribution, and wood volume for all 12 species, and estimates of mortality rates and lifetime growth patterns for the seven more common species.

With these data, we make preliminary assessments of the harvest potential of these species in natural forest using a simulation model of tree growth and mortality. Since we have no basis for modeling recruitment after a harvest (when most seed-producing trees would be removed), only residual stems ≥ 10 mm dbh were simulated. This produces information on about 120 years or so of future harvests. The model makes quantitative estimates of future productivity and assesses the effect of altering the cutting rotation (years between harvests) and the minimum dbh limit of harvest. Although crude, the model provides an approximate answer to the question: How much wood could be produced on a sustainable basis from these species in a natural forest?

Materials and methods

Species

Six of the species we chose to analyze were among the top ten native species in terms of wood volume harvested in Panama in 1987 (INRENARE 1990). The top three ranking species all occur in the plot - *Pochota quinata* (family Bombacaceae), *Prioria copaifera* (Leguminosae: Caesalpinoidae) and *Anacardium excelsum* (Anacardiaceae) - as do the eighth through tenth ranks - *Tabebuia rosea* (Bignoniaceae), *Calophyllum* *longifolium* (Guttiferae) and *Hura crepitans* (Euphorbiaceae). Four of the remaining six species that we chose to analyze are well known for timber elsewhere in Latin America but were not listed by INRENARE (1990) as top wood producers in Panama: *Cedrela odorata* (Meliaceae), the Spanish cedar (Enrique Vega 1987); *Platymiscium pinnatum* (Leguminosae: Papilionidae) and *Tabebuia guayacan*, valued in Panama for their hard, high-quality wood; and *Cordia alliodora* (Boraginaceae), a commonly used plantation species (Heuveldop *et al.* 1985,CATIE 1986, Nichols & Gonzales 1991). The final two species we analyzed were *Pochota sessilis*, a relative of the widely used *P. quinata* mentioned above, and *Enterolobium schomburgkii* (Leguminosae: Mimosidae), a close relative of *E. cyclocarpum*, a large tree of savanna land in Central America whose timber is prized for furniture and dugout canoes.

Five of the twelve species - *Anacardium, Cedrela, Enterolobium,* and both *Pochota* - had fewer than 25 individuals in the 50-ha plot, which we judged too few for analyses of growth rate and mortality, and we just provide information on their abundance and standing timber volume. The other seven species had 75 or more stems in the plot. Information on three of the 12 species - *Prioria, Enterolobium* and *Cordia* - based on this same dataset was published in Condit *et al.* (1993a, b).

Study site

The study was carried out in the tropical moist forest on Barro Colorado Island (BCI) in central Panama. Detailed descriptions of the climate, flora and fauna of BCI can be found in Croat (1978) and Leigh *et al.* (1982). Censuses of 50-ha of forest were carried out in 1981-1983, 1985, and 1990 (Hubbell & Foster 1983, 1986a, 1986b, 1990a, 1990b, 1992, Condit *et al.* 1992a, b; we refer to the first census, which lasted two years, as the 1982 census). All free-standing, woody stems ≥ 10 mm diameter at breast height (dbh) were identified, tagged, and mapped. The diameter of each stem was measured at breast height (1.3 m) unless there were irregularities in the trunk there, in which case the measurement was taken at the nearest lower point where the stem was cylindrical. If the trunk was buttressed, the diameter was taken above the buttresses (except in 1982, see below). In 1982 and 1985, a plastic plate with 0.5 cm increments was used to measure diameters of smaller stems (Manokaran *et al.* 1990), so that dbh of stems < 55 mm were effectively rounded down to the next smallest 5 mm multiple. In 1990, calipers were used and dbh's recorded to the nearest mm.

Estimating mortality

Mortality rates were calculated by dividing the number of dead stems in one census by the total living in the previous (Condit *et al.* 1995). Confidence limits for this fraction were calculated using the binomial variance and t- statistics, which are based on a normal approximation appropriate for sample sizes above 12 (Sokal & Rohlf 1973). To annualize mortality rates, the mean census interval for each species was calculated using the dates on which individual stems were censused. A standard exponential mortality model was used to calculate annual mortality, based on this mean time interval, and the same procedure allows the confidence limits to be annualized. For comparisons between census intervals and between species, confidence limits on mortality rates were calculated for all stems ≥ 10 mm dbh, or in two size classes, 10 - 99 mm and ≥ 100 mm, to see if larger stems had lower mortality rates than smaller (Condit *et al.* 1995).

Separate from mortality, we recorded plants whose main stem broke below 1.3 m but which survived and resprouted. In some cases it was not possible to tell whether the breakage occurred since the prior census or before it, so we counted stem-breakage only in cases where the later dbh was smaller than the earlier. Rates of stem-breakage were calculated exactly as were mortality rates. Note that stems broken above 1.3 m were not included in this definition of stem-breakage.

Estimating timber volume

The wood volume of each tree was estimated by multiplying basal area (pi times half the dbh squared) by height to the lowest branch. Height was measured with a range finder in six or seven individuals spanning the size range found in a given species, and from these the regression

$$\log_{10}(height) = a + b \log_{10}(dbh) \qquad \text{(Equation 1)}$$

was calculated. The equation allowed us to estimate the height of all individuals in the plot. O'Brien *et al.* (in prep.) gives tables of regression parameters for more than 50 species in the 50-ha plot; parameters for the species studied here were: *Calophyllum*, $a = -0.78$, $b = 0.74$; *Cordia*, $a = -0.40$, $b = 0.66$; *Platymiscium*, $a = -0.45$, $b = 0.60$; *Prioria*, $a = -0.98$, $b = 0.78$; *Pochota sessilis*, $a = -0.33$, $b = 0.61$; *Tabebuia guayacan*, $a = -0.40$, $b = 0.58$; and *T. rosea*, $a = -0.33$, $b = 0.61$ using dbh in mm, giving height in meters. Regressions were not calculated for *Hura*, *Anacardium*, *Cedrela*, *Pochota quinata*, or *Enterolobium schomburgkii* because of insufficient numbers of stems in certain size classes. For these species, a regression using combined height-dbh data from the other seven species was used: $a = -0.49$, $b = 0.64$.

This estimate is taken to be an approximation of how much wood could be harvested from an individual tree. We had to ignore stem form because we had no data on taper, and we had no information on wood volume in large branches or in the upper part of the stem. Two detailed studies of tropical trees (Yamakura *et al.* 1986, 1987) give an indication of the accuracy of our crude estimates. In 17 large trees from several families, actual bole volume averaged 14% lower than our method would estimate, but branch volume added as much or more than 14% to total wood volume (Yamakura *et al.* 1986). Thus, our method overestimates total wood availability by ignoring bole taper but underestimates it by ignoring large branches and the upper trunk. It is probably not much less accurate than typical regression methods (Dawkins 1961, Rai 1978, Pohjonen 1991).

Estimating growth

Dbh growth was estimated as

$$\frac{\ln\left(\frac{dhb_2}{dhb_1}\right)}{time} \qquad \text{(Equation 2)}$$

where dbh_2 is the later dbh and dbh_1 the earlier, *time* the interval between measures, and ln is the natural logarithm. This is referred to as instantaneous relative growth rate (Condit *et al.* 1993a) and is the correct method for estimating relative growth rate; the commonly used measure $\frac{1}{dbh_1}\frac{(dbh_2 - dbh_1)}{time}$ produces very nearly the same number in most cases, but is substantially in error when growth is rapid. In addition, in some cases dbh increments were calculated as $\frac{(dbh_2 - dbh_1)}{time}$. Because dbh was recorded in 5-mm intervals in 1982 and 1985 but to the nearest mm in 1990, it was necessary to round 1990 dbh's below 55 mm down to the next lowest 5-mm interval before calculating growth rates. All living stems which were not resprouts were included in growth calculations. Confidence limits of growth rates were based on standard t - statistics, which are appropriate for normal distributions, and growth distributions were reasonably normal. For comparisons of growth rates between censuses and between species, we calculated confidence limits on growth rates in doubling size classes: 10 - 19, 20 - 39, 40 - 79, 80 - 159, 160-319, 320 - 639, and ≥ 640 mm dbh. More size classes were used than for comparisons of mortality rates because growth rates varied substantially with stem size.

Rounding dbh's of smaller stems may bias growth estimates. Condit *et al.* (1993a) examined the magnitude of this inaccuracy and presented evidence that rounding dbh's will bias growth estimates downwards, but usually by less than 13%. We concluded that rounding dbh's to 5-mm intervals had relatively little impact on our estimates of mean growth rates.

A caution about estimates of growth and volume increments was raised by a few instances in which trees apparently had extreme growth or extreme shrinkage. In order to reduce the impact of a few erroneous dbh measures on growth estimates, we discarded all records of plants which shrunk by more than 5% of their initial dbh per year or grew by over 75 mm y^{-1}. Slight decrements, those less than 5% y^{-1}, were not excluded because they probably represented measurement errors on trees that did not grow; removing them would have biased growth rates upward. Excluding increments above 75 mm y^{-1} eliminated truly absurd errors but probably included the full range of legitimate growth rates in the species studied here (Condit *et al.* 1993a, b). Condit *et al.* (1993a) showed that mean growth rates calculated after excluding extremes were similar to median rates and were the most representative and unbiased way to present growth data.

Even after eliminating extremes, some erroneous measures remained in the datasets, especially among the large, buttressed trunks. For this reason, volume increments (which were dominated by the largest trees) and growth rates of the larger size classes must be viewed with some skepticism. The problem of errors in dbh measurements of large stems was compounded in 1982 by taking dbh measurements around buttresses, rather than above them (as was done in 1985 and 1990). Thus, volume estimates for 1982 were severe over-estimates and are not presented, and 1982-85 growth rates in the largest size classes were unreliable.

Projecting lifetime size trajectories

We recently developed a novel way to estimate lifetime dbh trajectories (Condit *et al.* 1993a) as an advance over earlier methods (Richards 1952, Valle 1979, Whitmore 1984, Lieberman & Lieberman 1985, Lieberman *et al.* 1985a, ter Steege 1990). The new method starts with a regression analysis to fit growth estimates as a continuous function of dbh, and then fits a second regression to the residuals about the first regression. The first regression provides an estimate of mean growth as a function of dbh, the second an estimate of the standard deviation (SD) of growth as a function of dbh. These curves are difference equations, but since time intervals between measurements were short, they approximate differential equations, relating the derivative of dbh on time to dbh.

Polynomial regressions relating instantaneous growth rates on natural log-transformed dbh were used, and the resulting differential equations were solved analytically, the solutions giving a function relating the dbh of a tree to its age (dbh-trajectory). There was one dbh-trajectory calculated from mean growth rates (based on the first regression curve), and one for growth one SD above the mean (based on the second). Because 10 mm dbh was the smallest size censused, the dbh-trajectories provided estimates of the time required to grow from 10 mm to any larger size. Condit *et al.* (1993a) described this technique in detail, showing the differential equations and their solutions.

Projecting lifetime survivorship

Survivorship to any given size was projected using the mean annual mortality rate for all stems, m (Condit *et al.* 1995). From this, the fraction of stems surviving to any time t (in years) was estimated as e^{-mt}. For each species and census period, we estimated survivorship to 100 mm, 300 mm, and 600 mm dbh, using the dbh-trajectories described above to find the time interval needed to reach these sizes. Because mortality rate did not vary significantly with size in any species, we projected survivorship using the mean mortality rate for all size classes. In three species we recalculated survivorship using separate mortality rates for stems < 100 mm and ≥ 100 mm in order to check the importance of the assumption of constant mortality at all sizes; results were very similar to those based on a single mortality rate.

Estimating recruitment

Recruits were defined as ingrowth into the census - stems ≥ 10 mm but < 80 mm dbh in one census that were not present in the prior census (Condit *et al.* 1992a). Apparent recruits that were ≥ 80 mm dbh were not counted as such because it was likely they were missed in the prior census. Recruitment rate was standardized by dividing the total number of recruits in one census by the number of adults in the previous census, then dividing by the mean census interval for the whole plot. Adults were defined as trees greater than the approximate minimum size of fruit production.

Harvest simulator

The dbh-trajectories produced by growth analyses consisted of mathematical functions relating dbh to age. For example, for *Prioria copaifera*, the equation for dbh as a function of age (1982-1985 data) was

$$\text{age} = \frac{\ln\left[\dfrac{k + \ln(10) + \dfrac{b}{2a}}{k - \ln(10) - \dfrac{b}{2a}}\right] - \ln\left[\dfrac{k + \ln(dbh) + \dfrac{b}{2a}}{k - \ln(dbh) - \dfrac{b}{2a}}\right]}{2ak} \qquad \text{(Equation 3)}$$

where $a = 4.12 \times 10^{-4}$, $b = -9.91 \times 10^{-3}$, and $c = 5.93 \times 10^{-2}$, and are parameters from the polynomial regression of growth on $\ln(dbh)$, and $k = \dfrac{b^2}{4ac} - \dfrac{c}{a}$ (Condit *et al.* 1993a). The future size of any stem ≥ 10 mm dbh can be calculated by applying Equation 3 and then a reverse version that gives dbh as a function of age. Because estimated growth rates for very large trees were sometimes unreliable, all growth was curtailed at 1250 mm dbh.

A simulation began by removing every tree above the dbh limit (300 or 600 mm) as the initial harvest. The volume of each remaining tree was then calculated from its projected dbh every 5 years into the future. When the time of the next harvest was reached (after 30 years or 60 years), all trees larger than the dbh limit were removed again. Natural mortality was applied after the total harvest volume was calculated by assuming a constant, exponential decay in wood volume. For example, if the projected harvest volume after 30 years without mortality was 5.0 m^3, and if annual mortality was 2%, then net harvest volume would be $5.0xe^{-0.02} \times 30 = 2.74$ m^3. Individual stems did not live or die; mortality occurred as if in an infinite (or very large) forest, with no stochastic elements. This approach obviated the need to simulate life or death of individual stems, and as long as mortality is independent of size (and it was in these species), it leads to perfectly legitimate estimates of mortality-caused volume loss.

Logging damage was modeled in a similar way. We assumed that 15% of non-harvested stems were killed during each logging cycle, and reduced the net harvest volume by a further 15% for each rotation (beyond the reduction due to natural mortality). In the example above, the 2.74 m^3 remaining after natural mortality was further reduced to 2.74 × 0.85 = 2.33 m^3 due to logging damage caused during the first harvest. After the second harvest, volume was reduced by 0.85 × 0.85 m^3, since each stem had to survive two harvests. The value of 15% was chosen to be optimistic relative to actual rates of damage (Johns 1988, Uhl & Guimarães Vieira 1989), but attainable with reasonable low-impact methods (Gullison & Harder 1993).

In the logging simulations, the mean 1982 - 1985 growth rate was used because it represented a period of moderately elevated growth apparently associated with the 1983 drought (Condit *et al.* 1992b); it might thus mimic the growth anticipated after logging opened the forest canopy. Mortality rates for 1982-1985 were used as well. Coupled with the damage level of 15%, we believe we are portraying a central or somewhat optimistic approximation of how much timber these seven species could yield over a 120-year period in the BCI forest. There is no doubt that the model is crude, but it is the best we have available right now.

Results

Abundance and size distribution

Prioria and *Calophyllum* had substantial populations in the 50-ha plot, with more than 900 stems each (Table 1). The other species were uncommon, with *Cedrela* and *Enterolobium* very rare and *Pochota quinata* having just a single living stem in 1990. Most of the species had a J-shaped size distribution that is typical of tropical forests (Kohyama 1991), with many more juveniles than adults, but *Hura* and *Anacardium* were exceptions, both having more large trees than small (Table 1). *Anacardium's* distribution was particularly top-heavy, with 15 of 24 stems above 1000 mm dbh and none below 40 mm (Table 1). The latter two species had the largest stems in the 50-ha plot: one *Anacardium* at 2790 mm dbh and one *Hura* at 2426 mm (in 1990).

Timber volume

Despite having very few stems in the 50-ha plot, *Hura* and *Anacardium* dominated the forest in terms of wood volume, with 44 and 25 $m^3\ ha^{-1}$ (Table 2). Only *Ceiba pentandra* (Bombacaceae) exceeded *Hura* in total volume in the 50-ha plot, with 46 $m^3\ ha^{-1}$. *Prioria* also had a substantial volume, with 22 $m^3\ ha^{-1}$. Two other species in the plot had over 20 $m^3\ ha^{-1}$: *Quararibea asterolepis* (Bombacaceae) with 40 $m^3\ ha^{-1}$ and *Trichilia tuberculata* (Meliaceae) with 25 $m^3\ ha^{-1}$. The remaining timber species listed in Table 2 each contributed less than 4 $m^3\ ha^{-1}$ of wood to the total forest volume of 537 $m^3\ ha^{-1}$.

Table 1. Number of stems in 13 dbh classes in the entire 50-ha plot, 1990. The total number of stems ≥ 10 mm dbh is given in the final column

Species	dbh (mm)													
	10-19	40-99	100-199	200-299	300-399	400-499	500-599	600-699	700-799	800-899	900-999	1000-1999	2000-2999	Total
Anacardium	0	2	0	0	0	0	1	2	1	2	1	14	1	24
Calophyllum	665	168	38	4	6	2	3	2	1	0	2	2	0	893
Cedrela	5	2	0	2	0	0	0	0	0	0	0	0	0	9
Cordia	43	16	19	21	13	5	2	0	0	0	0	0	0	119
Enterolobium	6	5	0	1	1	0	0	0	0	0	0	0	0	13
Hura	8	9	16	9	8	10	11	6	2	3	7	25	3	117
Platymiscium	165	37	18	12	4	9	7	8	5	0	1	0	0	266
Pochota quinata	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Pochota sessilis	8	4	4	3	1	1	1	1	0	0	0	0	0	23
Prioria	742	364	159	46	27	18	16	15	11	8	18	18	0	1 442
Tabebuia guayacan	29	16	5	4	3	4	2	2	2	2	1	3	0	73
Tabebuia rosea	189	58	35	15	8	4	3	5	0	0	0	1	0	318
Total forest	177 416	45 580	13 483	3 636	1 756	933	562	330	168	120	77	158	14	244 113

Despite the substantial standing volume in *Hura* and *Anacardium*, neither species accounted for much wood productivity; in fact, of the species analyzed here, only *Prioria* had an increment above 1 m^3 ha^{-1} from 1985 to 1990 (Table 2). The negative increments in *Anacardium* and *Tabebuia guayacan* were due to the relative inaccuracy of dbh measurements in the largest trees.

Table 2. Total volume, volume increments, and volume decrements, in m^3 per ha, over 1985-1990 (see text)

	1985	1985-1990		1990
	Volume	Increment	Decrement	Volume
Anacardium	24.56	- 0.32	0.03	25.30*
Calophyllum	2.46	0.45	0.31	2.61
Cedrela	0.01	0.00	0.00	0.02
Cordia	1.53	0.30	0.33	1.50
Enterolobium	0.01	0.02	0.00	0.03
Hura	43.08	0.95	0.01	43.94
Platymiscium	3.08	0.38	0.18	3.25
Pochota quinata	0.00	0.00	0.00	0.01
Pochota sessilis	0.31	0.15	0.00	0.46
Prioria	22.16	1.47	1.45	22.18
Tabebuia guayacan	3.75	- 0.06	0.00	3.10**
Tabebuia rosea	2.59	0.64	0.56	2.68
Total, 12 timber spp.	103.54	3.98	2.87	105.08
Total, entire forest	536.99	38.31	45.34	534.49

*initial volume plus increment minus decrement does not equal final volume because a single tree measured in 1990 was not measured in 1985

**initial volume plus increment minus decrement does not equal final volume because a single tree measured in 1985 was not measured in 1990 (even though it was still alive)

Mortality

Mortality rates for individual species were generally 2-3% y^{-1}, but with *Prioria* at just 0.5% and *Cordia* above 5% (Table 3). There were significant differences in mortality rates between species: *Prioria* in both census intervals and *Hura* and *Tabebuia guayacan* during 1985-90 had significantly lower mortality rates than *Calophyllum, Cordia, Platymiscium,* or *Tabebuia rosea* in either census period. Despite the fact that the forest as a whole had significantly higher mortality during 1982-85 than during 1985-90 (Condit *et al.* 1992b), none of these seven species did.

Mortality rate did not vary significantly with size in any species. In the two species with large sample sizes (*Calophyllum* and *Prioria*), differences in mortality between stems < 100 mm and ≥ 100 mm dbh were slight (Condit *et al.* 1995). Condit *et al.* (1993b) calculated mortality rates in several size classes in *Prioria* and found little variation.

Table 3. Rates of mortality and stem breakage of all dbh's combined, and projected survivorship to three different dbh's. For each species, the first row gives 1982-1985 data and the second 1985-1990 data. Sample size is given under *N*, followed by the number of stems that died and the annualized mortality rate (under the column labeled "mortality"), and then the number of broken stems and the annualized breakage rate (under the column labeled "breakage"). Projected survivorship gives the fraction of stems that would still be alive (of those beginning at 10 mm dbh) at three sizes, assuming mean growth, or mean plus one standard deviation in growth

	Stem loss rates					Projected survivorship					
						Mean growth			Mean+SD growth		
Species	N	Mortality		Breakage		10 cm	30 cm	60 cm	10 cm	30 cm	60 cm
Calophyllum	649	53	0.026	7	0.003	.266	.085	.029	.471	.242	.143
	722	82	0.023	17	0.005	.187	.038	.013	.385	.145	.077
Cordia	111	17	0.052	1	0.003	.155	.030	. . .	.426	.187	. . .
	108	14	0.027	3	0.005	.497	.189	. . .	.668	.360	. . .
Hura	127	7	0.015	2	0.004	.312	.163	.086	.580	.423	.317
	119	2	0.003	0	0.000	.830	.687	.547	.903	.820	.742
Platymiscium	256	23	0.029	14	0.017	.079	.001	.000	.307	.072	.032
	248	32	0.026	13	0.010	.049	.000	.000	.216	.032	.012
Prioria	1356	18	0.005	14	0.004	.743	.620	.549	.862	.770	.710
	1408	41	0.006	18	0.003	.640	.460	.349	.791	.651	.558
Tabebuia guayacan	76	5	0.021	1	0.004	.225	.082	.033	.516	.316	.202
	74	2	0.005	2	0.005	.659	.470	.303	.812	.687	.572
Tabebuia rosea	316	35	0.035	14	0.013	.043	.000	.000	.251	.035	.010
	299	33	0.022	20	0.013	.150	.013	.003	.374	.128	.073

Stem-breakage

Rates of stem breakage below breast height were always lower than mortality rates (Table 3). The vast majority of stem-breakage was in the smallest size class: of 126 stems that broke and resprouted in the seven species, 91 were < 20 mm dbh and 27 were 20-39 mm. The breakage rate among stems ≥ 40 mm, for all species combined, was below 0.1% in both census periods; for stems < 40 mm, the rate was 1.2% y^{-1}.

Dbh growth

Mean instantaneous relative dbh growth rates showed a consistent decline with tree size in all seven species (Figure 1 shows 1985-90 data; 1982-1985 data graphs had the same form). Six of seven species were similar to one another, with mean dbh growth of 4-6% y^{-1} at the smallest size falling to 1-2% by 150 mm dbh and then not changing much at larger sizes (Figure 1). *Cordia* was distinct, having mean dbh growth above 13% y^{-1} at small sizes but declining to zero at 450 mm dbh.

Despite the qualitative similarity of growth patterns in six species, there were significant differences. *Platymiscium* and *Tabebuia rosea* had mean dbh growth below 1% y^{-1} at sizes above 150 mm dbh, whereas *Calophyllum* and *Prioria* had rates closer to 2% (Figure 1). Dbh increments of 160-319 mm stems illustrate the magnitude of the differences: in 1982-85, *Calophyllum, Cordia,* and *Prioria* had dbh increments of 9.2, 7.1, and 8.6 mm y^{-1} respectively, all significantly higher than the growth of *Platymiscium* and *Tabebuia rosea,* (both 1.8 mm y^{-1}). In 1985-90, *Prioria* (mean 6.1 mm y^{-1}) and *Cordia* (4.7 mm y^{-1}) both grew significantly faster than *Tabebuia rosea* (1.5 mm y^{-1}), and *Prioria* alone grew faster than *Platymiscium* (1.4 mm y^{-1}).

Growth was significantly higher during 1982-1985 than during 1985-1990 in *Prioria* in the 320-639 mm and ≥ 640 mm dbh size classes (Condit *et al.* 1993b). It was higher but not significantly so in most other species (Figure 2). Condit *et al.* (1992b) showed that forest-wide growth was significantly higher during 1982-85 than during 1985-90 in all size classes above 40 mm dbh.

Growth rates one standard deviation (SD) above the mean showed the same pattern of size dependence as mean growth for all species; generally, mean+SD was about double the mean (Figure 1). In some species - *Calophyllum, Platymiscium,* and *Tabebuia rosea* - there were upturns in these growth curves in larger size classes, but these were probably artifacts caused by difficulties in dbh estimates of large trees.

Projected dbh-trajectories

The seven species showed three different types of dbh projections with age (Figure 2). *Cordia* had an S-shaped trajectory, with growth rate accelerating with age then slowing to a halt at around 450 mm dbh, a size which corresponds closely with the largest trees in the population (Table 1). It would take 60 years for *Cordia* to

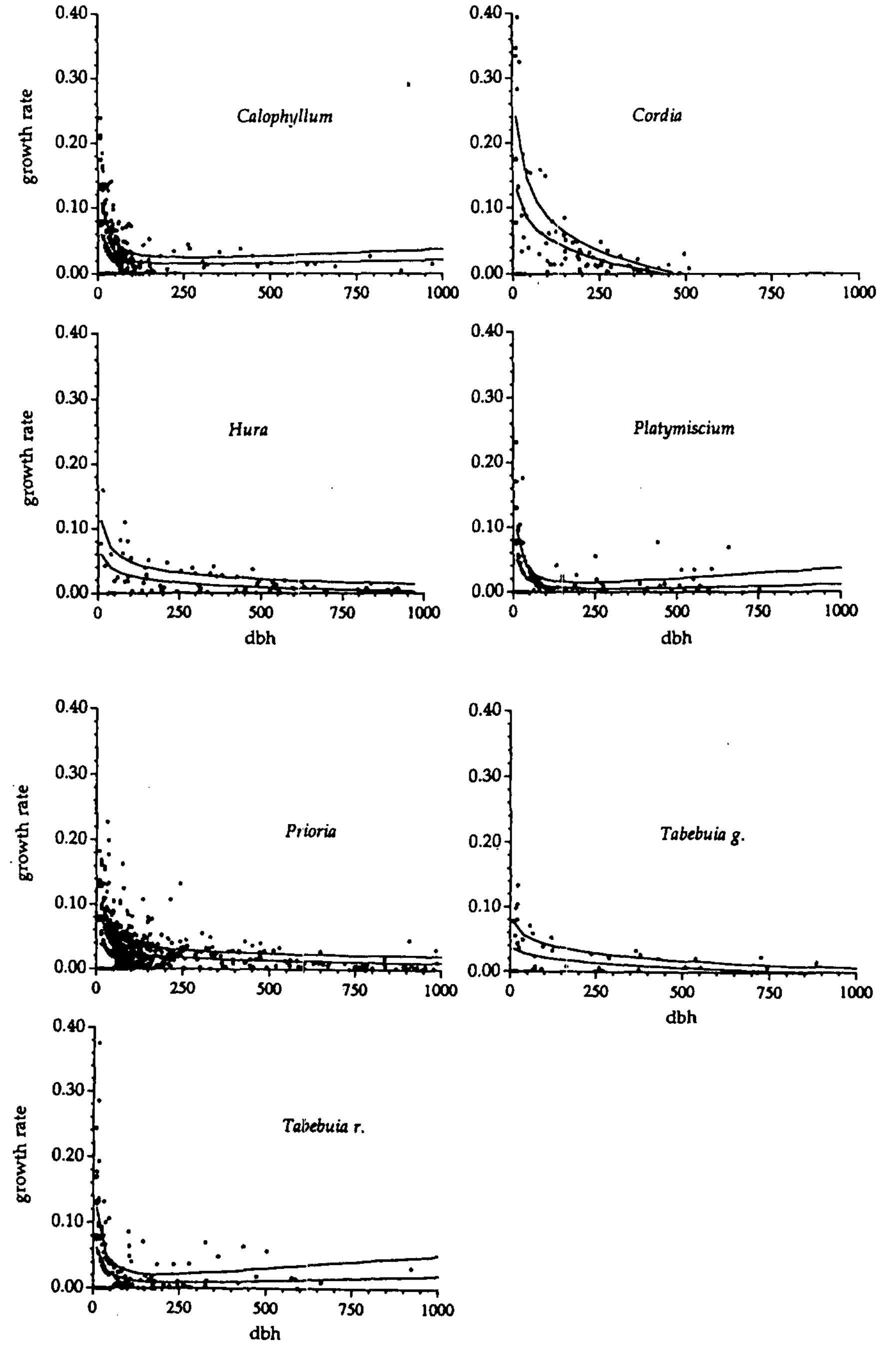

Figure 1. Annualized instantaneous relative dbh growth rates over 1985-1990 plotted against dbh in 1985. Each point represents one stem. The lower line was found as the best fit and represents mean growth. The upper line was found by adding the mean to the best fit of the residuals around the mean; it represents growth one standard deviation (SD) above the mean. Fiting was done using binomial regression of instantaneous growth on natural-log transformed dbh (see text and Condit *et al.* 1993b)

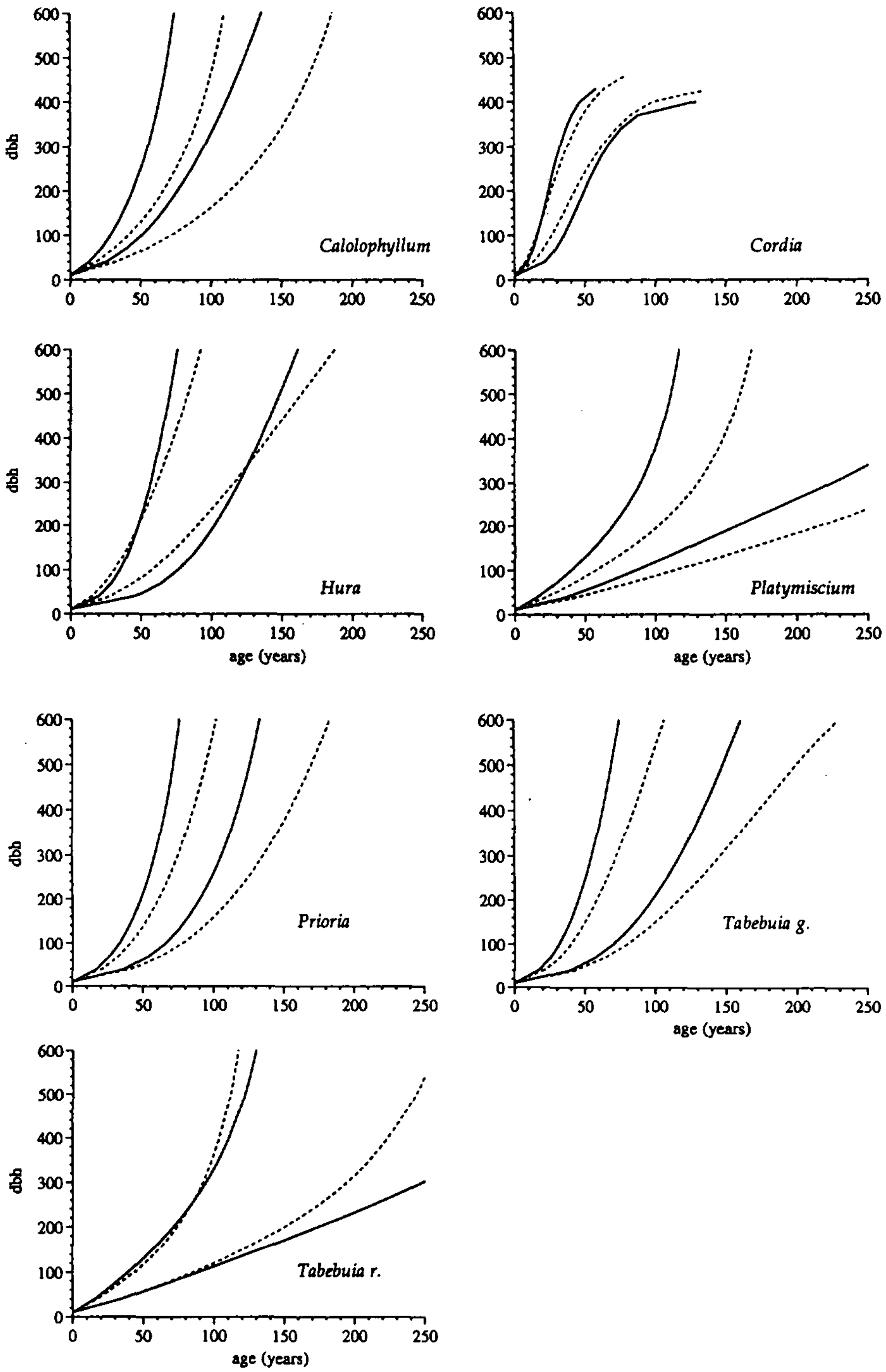

Figure 2. Projected growth of stems as a function of time since 10 mm dbh. The two solid lines are based on 1982-1985 data, the lower on mean growth and the upper on mean+SD growth. The two dashed lines give parallel results based on 1985-1990 data

reach 300 mm dbh at mean growth and 30 years at mean+SD growth. A second dbh-trajectory was seen in *Calophyllum, Hura, Prioria,* and *Tabebuia guayacan,* in which growth accelerated with dbh. These four species had roughly similar time courses in their growth, reaching 300 mm dbh in 100-150 years at mean growth, and 50-75 years at mean+SD growth (Figure 2). *Platymiscium* and *Tabebuia rosea* had dbh-trajectories similar in form to this second group, but had much slower growth rates. They took 200 years to reach 300 mm at mean growth, and 90 years at mean+SD growth (Figure 2).

Projected survivorship

Survivorship to 100 mm, 300 mm, and 600 mm dbh varied tremendously between species (Table 3). Species with lower mortality (*Hura, Prioria*) had > 50% of their stems survive to 300 mm dbh at mean growth or mean+SD growth (Table 3). At the other extreme, the two slow-growing species, *Platymiscium* and *Tabebuia rosea,* both of which had relatively high mortality rates, had survival of < 2% to 300 mm at mean growth and < 13% at mean+SD growth (Table 3).

Recruitment

Calophyllum had very successful recruitment over both census intervals, with a recruitment rate close to 3 recruits adult^{-1} y^{-1} (Table 4). At the other extreme, *Anacardium* and *Hura* had only one recruit between them over all eight years (Table 4).

Table 4. Recruitment in 1985 and 1990. The number of adults at the beginning of a census interval and the number of new stems < 80 mm dbh at the end are listed, then the recruitment rate (recruits per adult per year; see text). After the genus name for each species, the estimated reproductive size in mm dbh is given in parentheses

	1982-1985			1985-1990		
Species (reprod. size)	Adults	Recruits	Rate	Adults	Recruits	Rate
Anacardium (600)	19	0	0.00	19	0	0.00
Calophyllum (300)	14	135	2.86	17	259	2.90
Cedrela (300)	0	0	-	0	7	-
Cordia (200)	38	15	0.12	36	28	0.15
Enterolobium (400)	0	0	-	0	0	-
Hura (300)	72	1	0.00	74	0	0.00
Platymiscium (300)	40	30	0.23	37	58	0.30
Pochota quinata (300)	1	0	0.00	0	0	-
Pochota sessilis (300)	3	2	0.19	3	0	0.00
Prioria (600)	61	82	0.45	68	82	0.23
Tabebuia guayacan (300)	18	4	0.07	19	4	0.04
Tabebuia rosea (300)	29	37	0.38	23	59	0.48

Table 5. Simulated timber harvest (im m^3 per ha) based on mean growth rates and mortality rates from 1982-1985 data and assuming 15% mortality of all unharvested trees during each harvest. The first line for each species gives the projected harvest based on a 30-year rotation, the second line for a 60-year rotation. Under each year, the column for "300 mm" gives the harvest if all trees above 300 mm dbh were taken, and the column "600 mm" if a 600 mm limit were used. Blank entries indicate no harvest was attempted, whereas 0.00 means a harvest was scheduled but no trees above the limit were present. Total is the sum for just these seven species

	Year 0		Year 30		Year 60		Year 90		Year 120	
Species	300 mm	600 mm	300 mm	600 mm	300 mm	600 mm	300 mm	600 mm	300 mm	600 mm
Calophyllum	2.47	2.03	0.12	0.42	0.43	0.25	0.87	0.42	0.30	0.97
	2.47	2.03			0.71	0.80			2.10	1.94
Cordia	1.11	0.00	0.26	0.00	0.06	0.00	0.00	0.00	0.00	0.00
	1.11	0.00			0.14	0.00			0.00	0.00
Hura	43.82	42.17	0.29	2.07	0.14	0.81	0.07	0.47	0.01	0.14
	43.82	42.17			0.78	3.43			0.18	0.86
Platymiscium	3.06	2.02	0.05	0.29	0.01	0.06	0.01	0.02	0.00	0.00
	3.06	2.02			0.04	0.25			0.01	0.01
Prioria	21.53	19.16	1.00	3.76	1.93	3.34	2.45	4.69	3.15	6.86
	21.53	19.16			4.92	11.80			12.02	21.23
Tabebuia guayacan	3.03	2.65	0.09	0.38	0.05	0.22	0.04	0.06	0.04	0.09
	3.03	2.65			0.21	0.68			0.12	0.21
Tabebuia rosea	2.33	1.49	0.05	0.17	0.01	0.07	0.01	0.01	0.01	0.01
	2.33	1.49			0.04	0.19			0.01	0.01
Total	77.35	69.52	1.87	7.09	2.62	4.74	3.46	5.67	3.50	8.07
	77.35	69.52			6.86	17.14			14.43	24.28

Table 6. Total wood production (in m^3 per ha) over 120 years and fraction of the total coming from future harvests (years 30 to 120). Four different harvest schedules are compared, listed as rotation time then dbh limit. Total gives sums for just these seven species

Species	30-y 300-mm		30-y 600-mm		60-y 300-mm		60-y 600-mm	
	Total wood harvest	Future contribution	Total wood harvest	Future contribution	Total wood harvest	Future contribution	Total wood harvest	Future contribution
Calophyllum	4.19	.410	4.09	.503	5.28	.532	4.77	.575
Cordia	1.43	.224	0.00		1.26	.115	0.00	
Hura	44.33	.012	45.66	.076	44.78	.021	46.46	.092
Platymiscium	3.13	.023	2.39	.155	3.11	.016	2.28	.114
Prioria	30.07	.284	37.81	.493	38.47	.440	52.19	.633
Tabebuia guayacan	3.25	.069	3.41	.222	3.37	.100	3.54	.251
Tabebuia rosea	2.40	.029	1.74	.145	2.38	.021	1.69	.119
Total	88.80	.129	95.09	.269	98.64	.216	110.93	.373

Projected harvests

Initial harvests per ha were 42-44 m^3 for *Hura* and 19-22 m^3 for *Prioria*, accounting for 85% of the total (Table 5). (*Anacardium*,which would account for a high fraction of the initial harvest, was not included in the simulation.) Subsequent harvests were dominated by *Prioria* (Table 5). Using a 600-mm cutting limit and a 60-year rotation, one future *Prioria* harvest matched or exceeded the initial harvest (Table 5). *Calophyllum* was the only other species which had a future harvest close to the initial (Table 5). The fraction of total wood production after 120 years that came from future harvests was below 25% in the other five species, and in *Platymiscium, Hura,* and *Tabebuia rosea,* it was below 16% (Table 6).

The management schedule which produced the highest total wood volume - all species combined - over 120 years was a 60-year rotation combined with a 600-mm dbh limit (Table 6). This was largely due to *Prioria,* which produced 81 m^3 of wood from the 60-year-600-mm schedule and < 54 m^3 from the alternatives, and to *Hura* and *Tabebuia guayacan,* which also had maximum production from a 60-year-600-mm schedule (Table 6). For *Cordia, Platymiscium,* and *Tabebuia rosea,* maximum production came from the 30-year-300-mm schedule, and for *Calophyllum,* from the 60-year-300-mm schedule.

Discussion

The first main conclusion to draw from this analysis is how much demographic difference there was between species. We identified three different growth syndromes (fast, medium, and slow), two mortality patterns (high and low) and a range of dbh distributions, including species with no advance regeneration and those with plenty. These various patterns demand different management schedules, as illustrated by the harvest simulation. For example, *Cordia alliodora* had high growth and mortality and would have to be harvested on a 30-year, or possibly shorter, rotation, whereas *Prioria copaifera,* with low mortality, moderate growth, and large juvenile populations, would be better managed with a 60-year rotation and a larger cutting limit. This illustrates the need for managing individual species. If averages from the whole forest are taken to guide management, results would be well-suited for a few common species (that dominate the dataset), while rare species might be treated inappropriately. This does not necessarily require, however, different management schemes for every species. Indeed, a sensible approach would be to group species into a few demographic guilds and develop a management schedule for each guild.

In the harvest simulations, two species of seven produced reasonable amounts of timber in future harvests - *Calophyllum longifolium,* and *Prioria copaifera.* In these, growth was moderate, juvenile density high, and in *Prioria,* mortality very low. The simulation suggested that the remaining five species would not be good candidates for sustainable harvest in this forest. *Hura* had similar growth and mortality schedules to *Prioria,* but so few juveniles that future harvests were low compared to the first. The other species had moderate to low growth or high mortality, and despite substantial advanced regeneration, none produced much in future harvests. It would be difficult to justify leaving any timber behind to provide future harvests in these species.

Despite some obvious caveats and simplifications, which we discuss below, the simulation suggests some broad guidelines about how to manage timber. Our main recommendations and expectations are: 1) in fast-growing pioneers (like *Cordia*), a rotation on the order of 30 years is required, but for most timber species, rotations on the order of 60 years seem warranted; 2) species with little advanced regeneration will produce little in future harvests; 3) even with ample advanced regeneration, there are species with low growth rates (1% y^{-1} dbh growth at larger sizes) and high mortality rates (2-3% y^{-1}) that would produce so little in future harvests that it is unlikely they could be managed sustainably.

Using juvenile density - advanced regeneration - as an indicator of future harvest potential is a well-known forestry tool (Thang 1987), and our simulation provides justification for it. But as we emphasize in point three above, adequate advanced regeneration is not sufficient to assure good future harvests if growth is low and mortality high. Indeed, the importance of mortality in natural forest management seems to have been overlooked. Tropical forests generally have high mortality rates, often 2% y^{-1} (Lang & Knight 1983, Lieberman *et al.* 1985b, Lieberman & Lieberman 1987, Manokaran & Kochummen 1987, Swaine *et al.* 1987a, 1987b). In our study, *Tabebuia rosea* and *Platymiscium pinnatum* had mortality consistently at 2 - 3% y^{-1} - higher than their growth rates! Despite plenty of juveniles, they were the least productive species in the simulation. Conversely, the species with the lowest mortality - *Prioria copaifera* - was the most productive, highlighting the importance of mortality in forest management.

These general recommendations and conclusions were based on maximizing sustainable wood production, but ultimately the question of sustainability and harvest potential is an economic one. To an economist, wood produced after 60 or 120 years has a large discount attached to it. In fact, at even a 5% y^{-1} discount rate (absurdly low in Latin America), all future harvests shown in Table 5 would be so low that sustainable management would seem unfeasible - for example, the 21 m^3 per ha harvested from *Prioria* after 120 years would be worth only 0.05 m^3 per ha of current timber! We are not in a position to argue the merits of different discount rates, but simulations such as the one we present can form the basis for economic models. These may cast a new light on the trade-off between shorter versus longer rotations, or lower versus higher dbh limits. For example, although a 60-year rotation in *Prioria* was clearly optimal in terms of total wood production, a shorter rotation might be better if discounts are incorporated.

As for the caveats, we acknowledge that these simulations were based on several simplifying assumptions and must be taken as approximations. It is very important that we keep several assumptions in mind. First, we only ran simulations with mean growth rates from one period. We justify this by arguing that our interest is in the productivity of natural forest, and that mean growth rates within the forest are what we have to accept. Logging may increase growth by opening the canopy (this is why we used the slightly elevated growth rates of 1982-1985 rather than those of 1985-

1990), but we doubt the increase would be much if the forest were maintained in a somewhat natural state. Indeed, Primack *et al.* (1987) found little change in growth following logging in a natural forest. A second major assumption was that logging caused relatively little immediate damage (15% mortality) and no long-term damage. This was deliberately chosen to be optimistic but reasonable; obviously, predictions based on our simulation would be overestimates if damage were much more extensive.

Other simplifications in the model are probably of less consequence. For example, we did not model recruitment, but for 60 years and probably 120 years, this would have virtually no impact on harvests because few recruits would reach harvestable size in this period. We also curtailed tree growth at 1250 mm because data on larger sizes were unreliable, but fortunately, at mean growth rates, very few trees ever reached this limit during a 60 year rotation. Finally, we ignored several complications relating to growth rates: we did not take into account the interaction between mortality and growth in successive census intervals (Hubbell *et al.* 1991) nor the autocorrelation in growth between intervals (Condit *et al.* in prep.), and we ignored variation caused by local conditions or competitive interactions (Weiner & Solbrig 1984, Knox *et al.* 1989). We illustrated variation in growth by modeling dbh-trajectories from two census periods, with means and standard deviations, but in simulations we used just one curve, simply because it would have become very difficult to illustrate a range of harvest projections given all the variables at hand. We believe that the growth rate we used - the mean from the faster-growth interval - gave a reasonable central prediction of harvest potential. Incorporating further complexities would have been unwarranted given our current state of knowledge.

Despite the pitfalls, the simulation is the best predictor of sustainable yield we currently have available. It leads to some interesting general conclusions, principally that wood can be produced sustainably from some species which have adequate advanced regeneration and good growth and survivorship characteristics. Other species of timber trees, though, appear unable to produce reasonable wood qualities at typical harvest intervals given their natural growth and mortality schedules. The caveats and pitfalls that make these conclusions tentative also underscore the need for more detailed information about the demography of tropical forests and how forests will respond to changes brought about by logging or other human incursions.

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