

Identifying fast-growing native trees from the Neotropics using data from a large, permanent census plot

Richard Condit^{*,a}, Stephen P. Hubbell^{a,b}, Robin B. Foster^{a,c}

^aSmithsonian Tropical Research Institute, Latin American Program, P.O. Box 2072, Balboa, Panama

^bDepartment of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA

^cDepartment of Botany, Field Museum of Natural History, Chicago, IL 60605, USA

(Accepted 1 July 1993)

Abstract

To screen for rapidly growing trees, lifetime growth histories of 160 species were estimated from data collected in a permanent 50 ha census plot in tropical moist forest in Panama. Most of the 160 species had never been studied before in detail, and newly encountered species with rapid growth might provide better techniques for reforestation degraded soils in Central America. To estimate lifetime growth, polynomial regressions were fitted to instantaneous growth rates expressed as a function of log-transformed diameter at breast height (dbh). These functions represent a differential equation in dbh, and explicit solutions for the equations provided dbh trajectories as a function of age (starting at 1 cm dbh, which was the smallest size included in the census). Dbh trajectories were calculated for 160 species, and full growth data are presented for the 28 species that ranked among the fastest 15 to reach a dbh of 10, 30, or 60 cm. Dbh trajectories based on growth of one standard deviation above the mean were also estimated for these species by fitting a polynomial regression to the residuals around the original regression. The fastest-growing tree in the 50 ha plot was the balsa, *Ochroma pyramidale*, which reached 10 cm in 5 years and 30 cm in 10. *Cavanillesia platanifolia*, *Trema micrantha*, *Zanthoxylum belizense*, and *Vochysia ferruginea* were the other top-ranking species. At mean growth, the top 15 ranking species required 5–25 years to reach 10 cm, 10–67 years to reach 30 cm, and 32–111 years to reach 60 cm, starting at 1 cm. At growth one standard deviation above the mean, the same species required 4–18 years to reach 10 cm, 8–35 years to reach 30 cm, and 19–69 years to reach 60 cm dbh. We recommend that the little-known species from this list be further tested in reforestation trials.

Introduction

The faster forests in the tropics disappear, the greater the demand for reforestation degraded lands will be. Unfortunately, the natural regeneration of tree cover often takes place very slowly on badly degraded soils (Uhl, 1982; Uhl et al., 1982), and as a result there have been many attempts to hasten the

*Corresponding author.

process. Typically, monospecific plantations of *Pinus caribaea*, *Tectona grandis*, *Eucalyptus* spp., *Acacia mangium*, or one of a handful of other species are planted to reclaim degraded soils. We contend that these efforts have been restricted to only a few species simply because information on other species—optimum growth rates, source of seeds, techniques for storage and germination, etc.—has not been available.

This is unfortunate, because there is a vast diversity of tree species in the tropics, and many other species are probably suitable for plantation and reforestation. In Panama, for example, there are 2067 tree species (based on the computerized flora of Panama from the Missouri Botanical Garden, with some additions and modifications made from our experience), yet nearly all reforestation efforts involve only about 20 species, and only about half of these are native to the region (Instituto Nacional de Recursos Naturales Renovables (INRENARE), 1990). Surely there are many more fast-growing or potentially valuable trees among those 2067. Hundreds of tree species are utilized by local peoples in the tropics (Duke, 1968; Torres de Araúz, 1975; Saw et al., 1991), and in our surveys of tree use in a small village in Central Panama, 104 native tree species were identified as valuable. However, few of these trees have ever been used in reforestation projects.

There exist just a handful of attempts to evaluate substantial numbers of native tree species for their reforestation or plantation potential (Garcia Colmenarez, 1978; González et al., 1990; Espinoza and Butterfield, 1992). We are expanding these efforts by initiating an evaluation of the reforestation potential of native forest trees in Panama. The first phase of the evaluation is based on a permanent 50 ha census plot that was established in undisturbed forest on Barro Colorado Island in 1980 (Hubbell and Foster, 1983, 1992). The plot was established to provide large samples of individuals from many species, to allow estimates of demographic parameters across a wide range of size classes (Condit et al., 1993), and here we use the dataset to analyze information on the growth rates of 160 tree species, most of which have never before been studied. We develop a new method for estimating lifetime age-diameter trajectories which works effectively at smaller sample sizes than previous techniques demanded. With this method, we estimated the time it would take each species to reach 10, 30, and 60 cm in stem diameter and extracted the 28 fastest from the list. Both mean growth rates and accelerated growth rates were calculated, the latter on the basis of observed individual variation in growth (Condit et al., 1993).

Materials and methods

Study site

The study was carried out in tropical moist forest on Barro Colorado Island (BCI) in central Panama. Detailed descriptions of the climate, flora, and fauna

of BCI have been given by Croat (1978) and Leigh et al. (1982). Three censuses of the 50 ha plot were carried out—in 1981–1983, 1985, and 1990 (Hubbell and Foster, 1983, 1986a,b, 1990a,b, 1992; Condit et al., 1992a,b; we refer to the first census, which lasted 2 years, as the 1982 census). All free-standing, woody stems of 1 cm or more in 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 higher point where the stem was cylindrical. 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 of less than 55 mm were effectively rounded down to the next smallest 5 mm multiple. In 1990, calipers were used and dbh values recorded to the nearest millimeter.

Measuring growth

Growth rate was calculated as dbh increment, converted to an annual value using the time interval for a plant's quadrant. Because dbh values were rounded down in 1982 and 1985 but not 1990, it was necessary to round 1990 dbh values below 55 mm down to the nearest 5 mm interval before calculating growth rates. Rounding dbh values down by 5 mm may bias growth estimates of smaller stems, but Condit et al. (1993) calculated that the bias was minimal. All surviving stems which were not resprouts were included in growth calculations, except that, to reduce the impact of a few erroneous dbh measures on growth estimates, we discarded all records of plants which shrank by more than 5% of their initial dbh per year or grew by over 75 mm year⁻¹. Condit et al. (1993) used these cutoffs for estimating growth rates in *Prioria copaifera*, and found that they successfully eliminated the effect of highly erroneous measures and provided estimates close to the median.

Overview of the method for estimating dbh trajectories

Estimating long-term growth of tropical trees can only be done by extrapolating from shorter-term growth records, because most species do not have annual growth rings. Previous methods for extrapolating involved estimating growth rates from samples of trees in different size classes, then calculating the time it would take a tree to grow through successive size classes if it maintained mean growth (Richards, 1952; Del Valle, 1979; Whitmore, 1984; Ter Steege, 1990) or if it was assigned growth values from the observed distribution of growth estimates (Lieberman and Lieberman, 1986). Here we amend this technique, using regression analyses to fit growth estimates as a continuous function of dbh, then calculating instantaneous changes in dbh by treating the growth curve as a differential equation. The regression technique facilitates work with smaller sample sizes, as it can smooth out erratic fluctuations

in growth that result from small samples in individual size classes, and because it can be used to estimate growth rates for size classes lacking in the data.

We start by fitting a quadratic regression to data on instantaneous growth rates and log-transformed dbh, to provide an equation relating the derivative of the logarithm of dbh (with respect to time) to the logarithm of dbh. Log-transformation tended to enhance the fit of the regression at the smaller dbh values at the expense of fit at larger dbh values, because of the way logarithms compress the large values in a distribution and spread the small ones. We favored this trade-off because we were most interested in identifying rapid growth at smaller dbh values (up to 10 and 30 cm). Quadratic regression was used because it gave improved fit over linear regression; higher-order polynomials would have given even better fits, but did not allow explicit solutions to the resulting differential equation.

Solving the growth equation

We let D be the dbh and $L = \ln(D)$ be the natural logarithm of dbh. We can define the growth rate, g , as

$$g = [\ln(D_t) - \ln(D_0)]/t = (L_t - L_0)/t \quad (1)$$

where subscripts t and zero denote measures taken at time t at time zero, respectively. As t approaches zero, dL/dt approaches g . For each plant, g was measured in the field and used as an estimate of dL/dt . This is an approximation, because the latter is an instantaneous measure of growth whereas the former is not, but the approximation is justified because the time intervals used were 3–5 years, which is short in terms of how fast most trees grow. The growth rate, g , is based on a standard exponential equation for plant growth; it is not the same as relative growth, which is $(D_t - D_0)/(D_0 t)$ (Welden et al., 1991; Condit et al., 1993), but at low growth rates the two differ only slightly.

Growth is expressed as a function of dbh by the following equation:

$$g = dL/dt = aL^2 + bL + c \quad (2)$$

This equation is found by modeling growth as a quadratic function of L , obtaining the parameters a , b and c using a standard polynomial regression exercise, with each stem providing a single point—estimates of g and L . An explicit solution to Eq. (2) can be found by direct integration (Purcell, 1972); it takes different forms for different parameter values. If $b^2/4a^2 < c/a$ and $a \neq 0$, then, letting $k^2 = c/a - b^2/4a^2$, the solution is

$$t = (1/ak) \arctan[(L + b/2a)/k] + m \quad (3)$$

If, on the other hand, $b^2/4a^2 > c/a$ and $a > 0$, and letting $k^2 = b^2/4a^2 - c/a$, the solution becomes

$$t = (1/2ak) \ln[(L + b/2a - k)/(L + b/2a + k)] + m \quad (4)$$

Lastly, if $b^2/4a^2 > c/a$ but $a < 0$, again letting $k^2 = b^2/4a^2 - c/a$, then

$$t = -(1/2ak) \ln[(L + b/2a + k)/(-L - b/2a + k)] + m \quad (5)$$

The constant m is the constant of integration and is found by setting initial conditions, which in our case were $t=0$ at $L=\ln(1 \text{ cm})$, as the census began with trees at 1 cm dbh. There are actually further solutions to Eq. (1) for the conditions $a=0$ or $b^2/4a^2=c/a$, but these exact equalities would never be encountered when fitting parameters to real data.

The solutions in Eqs. (3)–(5) give a dbh trajectory—the relationship between size and age. They express age as a function of time, but they could easily have been rearranged to express dbh as a function of age. As we wished to calculate the age at which the average tree would reach 10 cm, 30 cm, and 60 cm dbh, we kept the former. For each species, we solved for the parameters a, b , and c , used the natural logarithm of the three sizes, and found three ages.

These equations give mean performance of a species because they were based on mean growth rates. To estimate performance one standard deviation above the mean, we fitted a polynomial curve to the residuals of growth rate relative to the original growth equation (Eq. (2)), where the residual r was defined as the absolute value of the observed minus the fitted growth rate (Eqs. (1) and (2)):

$$r = |g - (aL^2 + bL + c)| \quad (6)$$

A second differential equation was then written for each species based on $g' = g + r$, the mean growth rate plus the residual:

$$g' = a'L^2 + b'L + c' \quad (7)$$

A second set of constants, a' , b' , and c' , was fitted for each species, and solutions for Eq. (7) were found (as in Eqs. (3)–(5)). These give the dbh trajectory of a tree which grew consistently one standard deviation above the mean. Rather than referring to this more rapid trajectory repeatedly as ‘growth one standard deviation above the mean’, we call it simply ‘accelerated growth’.

It is necessary that growth rates be zero or higher for the solutions in Eqs. (3)–(5) to hold. Thus, for any species for which the fitted growth rates g or g' fell to zero at any $\text{dbh} > 1 \text{ cm}$, we assumed the tree stopped growing at that size. On the other hand, if $g < 0$ at $\text{dbh} = 1 \text{ cm}$, we made no calculations for the species. A mean growth rate below zero is biologically unreasonable, but it is statistically possible: it happened for 12 species with small sample sizes (less than 10).

Selecting the fastest-growing species

A total of 185 tree species have been recorded in the 50 ha plot (including canopy and medium-sized trees as defined by Hubbell and Foster (1986a)). As a polynomial regression demands three points, we excluded species for which sample sizes for growth estimates were below three. Five palm species were also omitted because palms do not have true diameter growth. Species names used here follow Croat (1978).

For the remaining species, the time it took to reach 10 cm, 30 cm, and 60 cm dbh (starting at 1 cm) was calculated for each census interval, using the mean growth curve. There were 160 tree species whose predicted trajectories reached 10 cm dbh, 139 which reached 30 cm, and 130 which reached 60 cm. We constructed rankings based on these times—six in all because there were three sizes and two censuses—and from each, the fastest 15 species were extracted. After the rankings were made, five species had their rankings for the 60 cm size cutoff removed because no individuals in the plot were larger than 45 cm dbh (species which had at least one stem above 50 cm kept their ranks for growth to 60 cm). One other species was removed from the 1982–1985 list because its records for rapid growth were all errors (see below). The remaining species were combined into a single list, and this is the group for which we present detailed data, including mean and accelerated growth (separate rankings of accelerated growth rates were not made, however). A histogram of the mean time to reach the three size cutoffs among the species is provided as well.

Checking for errors

Screening a large dataset for extreme records tends to concentrate erroneous measures, so we were careful to guard against erroneous estimates of rapid growth. Having two consecutive growth estimates greatly strengthens our ability to judge the validity of individual records (Condit et al., 1993). For example, some cases of extreme growth could be judged as obviously invalid, such as the (real) case where dbh was recorded at 64 cm in 1982, 45 cm in 1985, then 57 cm in 1990; indeed, we removed one species from the high-ranking list because all its rapid growth records were erroneous in this obvious fashion. On the other hand, records where growth rate was very high in both census intervals were considered legitimate, as the probability of consecutive mis-measures would be low (Condit et al., 1993). This allowed us to conclude that some records of growth above 60 mm year^{-1} were legitimate, but that there were no clearly legitimate growth rates above 75 mm year^{-1} . Of course, there were erroneous growth estimates below 75 mm year^{-1} , and we checked carefully for such errors in data from the top-ranking species.

Results

The fastest-growing species

Twenty-eight species of trees were included in the list of top ranking growth rates, representing the top 17.5% of the 160 species analyzed (Table 1). The fastest-growing tree was the balsa, *Ochroma pyramidale*, which had the top rank in four of six categories (Table 1). The other species ranking near the top were *Cavanillesia platanifolia*, *Trema micrantha*, and *Zanthoxylum belizense*, which each had at least two rankings in the top three; *Vochysia ferruginea* had the last top rank (Table 1). These were the only five species that reached any of the dbh cutoffs at a mean rate of better than 1 cm year^{-1} (Table 1). A few other species achieved 1 cm year^{-1} accelerated growth: *Inga punctata*, *I. marginata*, *Ocotea puberula*, and *Jacaranda copaifera* (Figs. 1(B) and 2(B)). Figures 1–3 illustrate complete dbh trajectories for these species and some of the others with top rankings; Figs. 1 and 2 include both mean and accelerated trajectories.

Time course of dbh trajectories

Simulated trajectories based on mean growth rates for all 160 species reached 10 cm dbh in 5–120 years (Fig. 4(A)), with a few species taking longer (as long as 695 years). The top 15 ranking species required 5–23 years in 1982–1985 and 7–25 years in 1985–1990 (Table 1). Accelerated growth for the same 15 species reduced this time to 4–18 years, and again slightly longer in 1985–1990. To reach 30 cm dbh required 30–250 years for most species, with the top 15 ranking species requiring 10–67 years at mean growth and 8–35 years at accelerated growth. Thus the fastest-growing species reached both 10 and 30 cm averaging well over 1 cm year^{-1} , but the 15th ranking species averaged about 4 mm year^{-1} .

To reach 60 cm, most species needed 70–400 years at mean growth (Fig. 4(C)). The fastest growing species required 60 years when 1985–1990 data were used (*Vochysia*), but 32 years with 1982–1985 data (*Trema*, see Table 1). (Ranks 1 and 2 are missing from 1982–1985 data because these two species were dropped from the 60 cm list.) The same two species reached 60 cm in 39 years and 19 years, respectively, at accelerated growth. The 15th ranking species required 85–111 years to reach 60 cm dbh with mean growth (Table 1), or 45–69 years at accelerated growth.

Form of dbh trajectories

Some trajectories indicated growth rates that decreased with age, for example, *Cecropia obtusifolia* and *Cavanillesia* with 1982–1985 data (Fig.

Table 1
Growth trajectories of 28 fast-growing tree species

Species (largest dbh)	Age at			Rank			Regression parameters			r^2
	10 cm	30 cm	60 cm	10 cm	30 cm	60 cm	a	b	c	
<i>Annona spraguei</i> (35)	19.9	-	-	12	-	-	5.98e-3	-0.117	0.467	0.317
	24.6	82.6	...	13	26	...	1.33e-2	-0.166	0.526	0.498
<i>Apeiba tibourbou</i> (40)	21.0	104.9	...	13	46	...	4.22e-2	-0.451	1.210	0.420
	16.0	69.6	...	6	18	...	2.33e-2	-0.287	0.888	0.416
<i>Cavanillesia platanifolia</i> (248)	7.3	21.5	72.7	2	3	9	3.18e-2	-0.434	1.480	0.756
	16.2	35.6	60.7	7	4	2	8.00e-3	-0.124	0.483	0.380
<i>Cecropia insignis</i> (64)	18.4	100.6	137.3	11	43	36	3.94e-2	-0.433	1.200	0.560
	17.1	63.0	96.0	8	12	9	3.15e-2	-0.357	1.030	0.709
<i>Cecropia obtusifolia</i> (31)	12.6	-	-	6	-	-	2.47e-2	-0.328	1.060	0.842
	13.1	-	-	4	-	-	2.96e-2	-0.369	1.140	0.938
<i>Ceiba pentandra</i> (242)	18.1	106.8	-	10	51	-	1.46e-2	-0.200	0.665	0.505
	32.8	69.5	113.8	25	17	16	3.57e-3	-5.66e-2	0.228	0.354
<i>Cordia alliodora</i> (59)	34.9	66.0	-	30	20	-	-1.20e-2	8.52e-2	-7.96e-2	0.087
	26.3	62.0	-	18	11	-	-1.56e-3	-2.06e-2	0.183	0.274
<i>Guazuma ulmifolia</i> (94)	37.7	71.6	-	37	24	-	-5.59e-3	3.12e-2	2.31e-2	0.123
	49.7	75.3	102.7	43	22	11	-6.25e-3	5.04e-2	-4.98e-2	0.124
<i>Hampea appendiculata</i> (41)	15.0	38.3	...	7	6	...	2.33e-2	-0.276	0.849	0.353
	22.3	49.9	-	9	7	-	-2.66e-2	0.195	-0.239	0.572
<i>Inga coelestis</i> (31)	30.1	56.1	...	21	12	...	-4.97e-3	2.22e-2	6.21e-2	0.034
	28.9	74.6	-	20	20	-	1.20e-3	-4.44e-2	0.225	0.140
<i>Inga marginata</i> (51)	34.7	58.1	106.1	29	14	19	-8.16e-3	5.8e-2	-3.27e-2	0.010
	35.3	58.1	77.1	29	9	4	-1.03e-3	-1.52e-3	8.38e-2	0.015
<i>Inga punctata</i> (34)	17.4	42.5	-	9	8	-	-6.59e-3	5.22e-3	0.201	0.379
	22.9	48.1	...	10	6	...	1.01e-2	-0.125	0.420	0.311
<i>Inga spectabilis</i> (40)	43.9	78.8	-	48	31	-	-9.36e-3	6.77e-2	-6.54e-2	0.150
	25.6	63.8	-	16	13	-	-6.14e-3	1.8e-2	0.107	0.395
<i>Jacaranda copaia</i> (136)	26.3	46.4	67.6	18	9	7	-1.80e-3	-4.63e-3	0.127	0.125
	25.3	52.8	92.3	15	8	8	2.43e-3	-5.29e-2	0.249	0.315

<i>Laetia procera</i> (61)	16.7	61.9	100.2	8	17	17	2.97e-2	-0.341	0.996	0.550
	33.6	86.2	147.9	28	28	30	7.98e-3	-0.101	0.332	0.409
<i>Lafoensia punicifolia</i> (68)	23.1	47.3	78.4	15	10	12	2.88e-3	-5.88e-2	0.273	0.695
	14.8	67.7	268.4	5	16	77	2.61e-2	-0.320	0.984	0.969
<i>Ochroma pyramidale</i> (44)	4.7	10.2	...	1	1	...	0.324	-3.110	7.61	0.941
	7.6	19.0	...	1	1	...	1.27e-2	-0.242	1.01	0.985
<i>Ocotea oblonga</i> (51)	35.1	59.5	84.8	31	16	15	-2.75e-3	1.10e-2	6.21e-2	0.027
	33.3	67.2	111.0	27	15	14	1.51e-3	-3.59e-2	0.178	0.153
<i>Ocotea puberula</i> (51)	38.2	56.9	70.9	38	13	8	-3.34e-3	2.71e-2	8.03e-3	0.002
	49.4	75.0	85.8	42	21	5	1.02e-2	-8.98e-2	0.233	0.055
<i>Pourouma guianensis</i> (37)	32.0	55.6	-	22	11	-	-1.61e-2	0.122	-0.149	0.071
	31.4	65.5	...	23	14	...	1.13e-2	-0.126	0.381	0.302
<i>Pseudobombax septenatum</i> (151)	59.2	417.6	...	78	124	...	5.95e-3	-7.54e-2	0.237	0.399
	23.6	59.5	111.3	11	10	15	9.20e-3	-0.124	0.427	0.942
<i>Simarouba amara</i> (78)	36.6	64.3	83.3	35	19	13	4.36e-3	-5.22e-2	0.193	0.058
	38.6	76.0	103.6	31	23	12	5.84e-3	-7.01e-2	0.236	0.153
<i>Solanum hayesii</i> (30)	24.2	59.5	...	16	15	...	2.25e-2	-0.243	0.684	0.342
	25.6	-	-	17	-	-	6.69e-3	-1.64e-3	0.190	0.349
<i>Spondias mombin</i> (92)	21.9	106.3	130.6	14	50	30	4.13e-2	-0.440	1.180	0.553
	25.0	324.7	490.7	14	117	105	2.67e-2	-0.300	0.845	0.568
<i>Trema micrantha</i> (73)	7.5	23.1	32.4	3	4	3	7.36e-2	-0.818	2.330	0.813
	10.6	21.4	-	2	2	-	3.11e-2	0.201	-9.12e-2	0.808
<i>Turpinia occidentalis</i> (56)	34.0	81.5	109.3	28	33	22	1.38e-2	-0.152	0.439	0.200
	24.1	97.8	182.1	12	33	42	1.91e-2	-0.224	0.665	0.521
<i>Yochysia ferruginea</i> (51)	26.4	39.6	48.3	19	7	4	5.04e-4	1.90e-3	8.70e-2	0.001
	27.9	48.1	60.4	19	5	1	8.03e-3	-8.69e-2	0.288	0.131
<i>Zanthoxylum belizense</i> (106)	10.6	28.9	48.4	5	5	5	3.05e-2	-0.373	1.170	0.593
	12.2	30.8	99.4	3	3	10	1.13e-2	-0.180	0.695	0.657

For each species, the first row of data is based on the 1982–1985 census period and the second on the 1985–1990 census period. The largest dbh refers only to the 50 ha plot. Projected age (in years) to reach three different dbh values is given, followed by the rank in these ages, with Rank 1 indicating the fastest growth. The symbol ‘-’ indicates that the fitted growth rate fell to zero before the indicated dbh, and ‘...’ indicates that the projection to 60 cm was excluded because the largest tree was well below 60 cm dbh. Separate rankings were made for 1982–1985 and for 1985–1990, hence there are two Rank 1s at each size, etc.; however, a few ranks are missing because species were removed after the rankings were constructed (see text). The last four columns give the parameters for the polynomial regressions; a , b , and c are from Eq. (2) in the text.

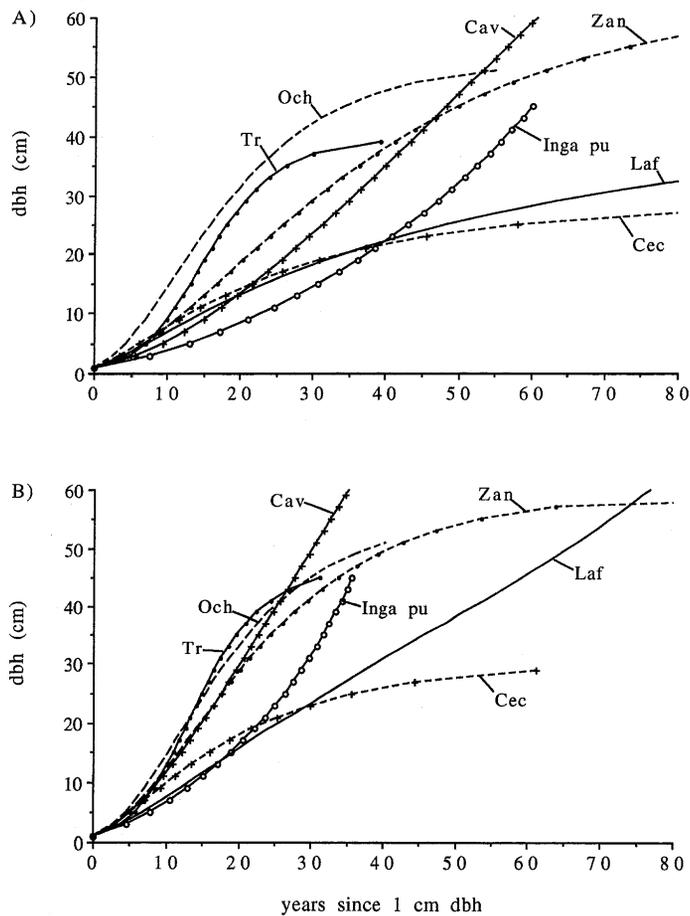


Fig. 1. Simulated dbh trajectories of the five fastest species to reach 10 cm dbh and 30 cm dbh; seven species are shown because two of the fastest to reach 10 cm were not among the top five to reach 30 cm. (A) Based on 1985-1990 mean growth curves. (B) Based on 1985-1990 accelerated growth curves. Tr, *Trema*; Och, *Ochroma*; Cav, *Cavanillesia*; Zan, *Zanthoxylum*; Inga pu, *I. punctata*; Laf, *Lafoesia punicifolia*; Cec, *Cecropia obtusifolia*.

3(A)), or *Ochroma*, *Trema*, *Zanthoxylum*, *C. obtusifolia* and *Lafoesia* in 1985-1990 (Fig. 1). Others showed growth rates that increased with age, such as *Ocotea puberula* (Figs. 2 and 3). In some cases, changes in growth rate were so slight that trajectories were essentially a straight line, and other trajectories had a slight sigmoid shape, with initially increasing then subsequently decreasing growth (*Trema* in Fig. 1, for example). The form of a growth curve for a given species was not consistent between census periods; for example, several species that had accelerating growth trajectories in 1982-1985 had sigmoid curves in 1985-1990. However, trajectories based on ac-

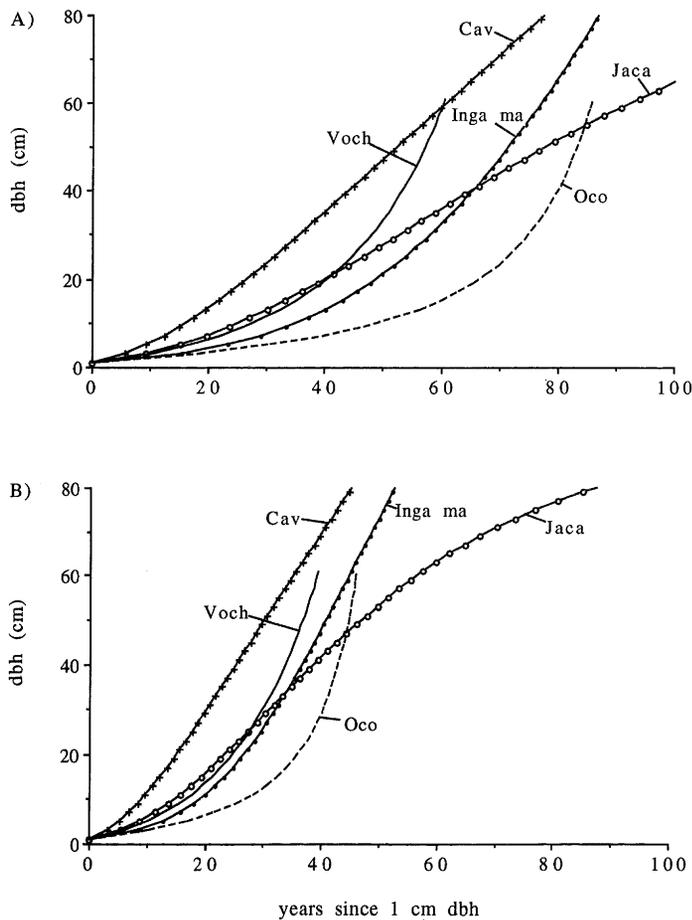


Fig. 2. Simulated dbh trajectories of the five fastest species to reach 60 cm dbh. (A) Based on 1985–1990 mean growth curves. (B) Based on 1985–1990 accelerated growth curves. Cav, *Cavanillesia*; Voch, *Vochysia ferruginea*; Inga ma, *I. marginata*; Jaca, *Jacaranda*; Oco, *Ocotea puberula*.

celerated growth rates had the same form as those based on mean growth (Figs. 1 and 2). Raw growth rates in two size classes (1–10 cm dbh and 10 cm dbh or more) for all 28 of the fast-growing species are provided in Table 2; mean, median, and maximum growth rates along with sample sizes are listed.

Fit of the regressions

For species with reasonably large sample sizes, regression curves fitted the

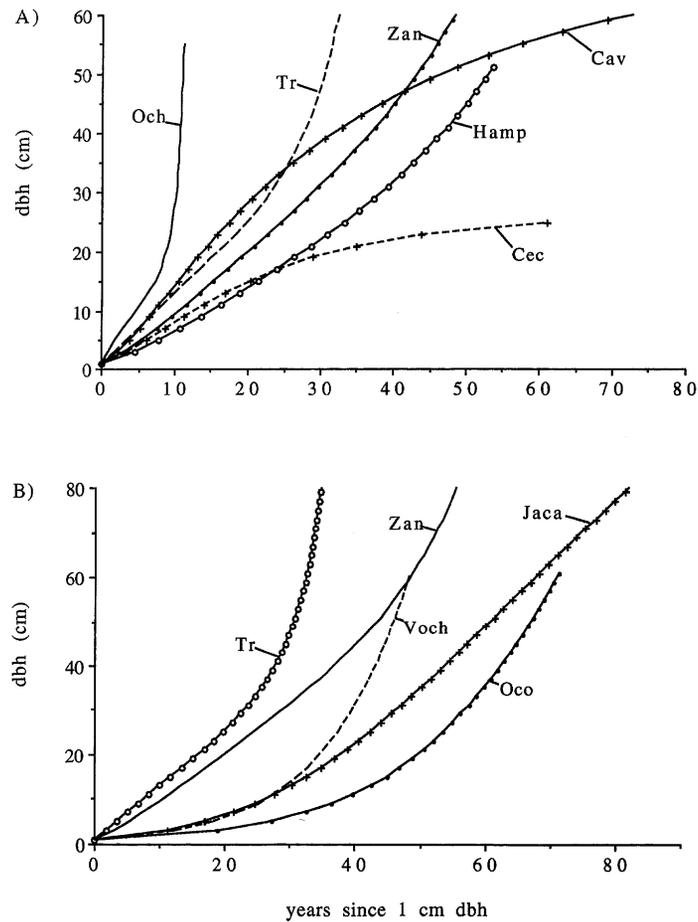


Fig. 3. Simulated growth trajectories for 1982–1985 data, mean growth curves only (accelerated curves for 1982–1985 are not shown). (A) The five fastest species to 10 cm and to 30 cm dbh (six species all told are shown). (B) The five fastest to reach 60 cm dbh. Och, *Ochroma*; Tr, *Trema*; Zan, *Zanthoxylum*; Cav, *Cavanillesia*; Hamp, *Hampea*; Cec, *Cecropia obtusifolia*; Jaca, *Jacaranda*; Voch, *Vochysia ferruginea*; Oco, *Ocotea puberula*.

growth data very well (Figs. 5(A) and 5(B)). In some cases, r^2 was very low, but this reflected variation in growth within dbh classes, not a failure of the curves to match the data (parameters for the regressions are given in Table 1). Data from *Ocotea oblonga* illustrate this well: r^2 was essentially zero (Fig. 5(B); Table 1), but the fitted curve matched the mean growth rate closely at all sizes. The fit for *Zanthoxylum* was equally good (Fig. 5(A)). *Trema micrantha* (Fig. 5(C)) illustrates the fit for a fast-growing but rare species. The regression curves fit the data well, but the curves for the two different cen-

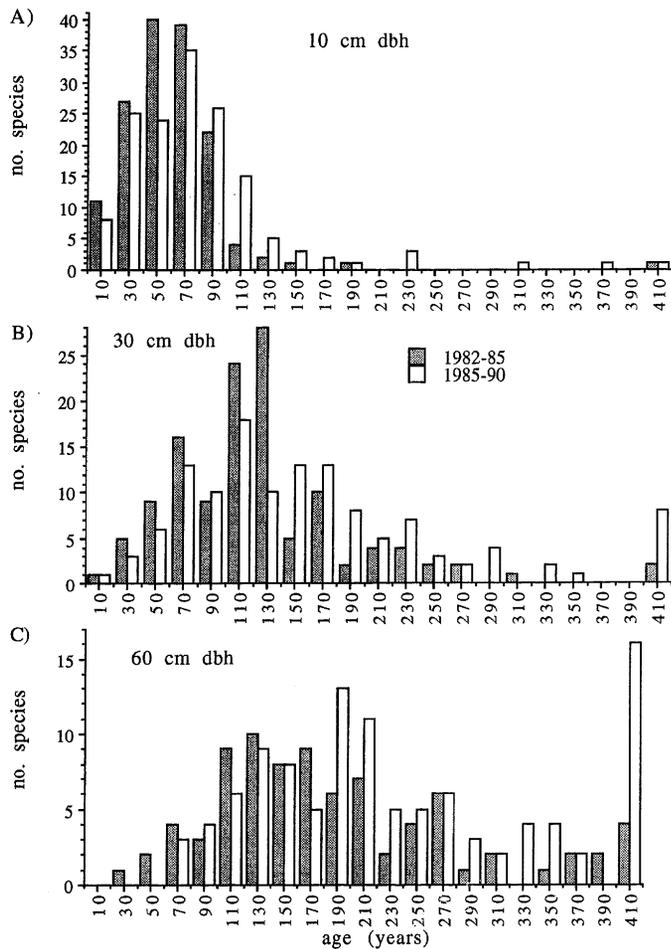


Fig. 4. Histogram of the time to grow from 1 cm to (A) 10 cm dbh, (B) 30 cm dbh, and (C) 60 cm dbh, in all species analyzed (see text).

suses had very different forms, largely as a result of the lack of any plants of less than 3 cm dbh in 1985. Despite the difference, the projected growth trajectories for the two census intervals were similar (Table 1).

The regression technique did yield a few aberrant dbh trajectories. Indications of peculiar fits can be seen in cases where 1982-1985 data and 1985-1990 data predicted vastly different ages at a given size, but where growth rates (Table 2) were not so different in the two census periods. The clearest examples were *Lafoensia* and its time to reach 60 cm dbh, and *Spondias* and its time to 30 cm and 60 cm. In these cases, data were lacking over intermediate sizes, and the fitted curves interpolated very differently in the two census periods. Other than these few cases, the polynomial fits were good; growth

Table 2
Growth rates of 28 fast-growing species

Species	Family	1–9.9 cm dbh					> 10 cm dbh				
		<i>n</i>	Mean	SD	Median	Maximum	<i>n</i>	Mean	SD	Median	Maximum
<i>Annona spraguei</i>	Annonaceae	24	4.8	5.3	2.9	17.2	16	5.4	4.0	3.8	14.5
<i>Apeiba tibourbou</i>	Tiliaceae	37	5.5	4.9	4.7	18.0	16	3.7	2.6	2.8	8.4
<i>Cavanillesia platanifolia</i>	Bombacaceae	15	5.1	6.1	1.8	19.9	21	4.2	4.4	3.2	12.2
		12	9.6	11.6	3.7	37.3	14	4.9	5.2	3.8	17.3
		1	27.8	0.0	27.8	27.8	18	8.0	21.5	6.7	52.2
		0	–	–	–	–	20	13.4	13.9	11.5	42.6
<i>Cecropia insignis</i>	Moraceae	101	6.1	7.2	3.5	36.1	217	4.7	9.8	4.4	42.5
		82	9.7	8.4	7.2	29.1	206	6.1	5.7	4.8	31.0
<i>Cecropia obtusifolia</i>	Moraceae	3	15.2	12.4	9.9	29.4	22	3.5	3.9	3.3	10.8
		6	15.3	6.2	14.5	26.1	15	3.3	2.7	2.8	8.1
<i>Ceiba pentandra</i>	Bombacaceae	20	6.6	6.9	4.2	27.5	24	–7.2	23.5	1.0	47.3
		17	4.3	5.9	2.0	23.2	26	7.5	23.3	2.6	73.7
<i>Cordia alliodora</i>	Boraginaceae	37	3.4	6.2	0.0	22.9	53	4.8	8.1	4.5	19.1
		38	4.9	6.1	2.8	21.0	53	4.9	4.3	3.9	16.4
<i>Guazuma ulmifolia</i>	Sterculiaceae	21	3.6	5.2	1.9	21.6	20	4.9	11.6	4.9	34.6
		12	2.2	2.5	1.1	7.0	29	10.8	11.4	10.7	32.7
<i>Hampea appendiculata</i>	Malvaceae	12	7.9	7.1	6.8	20.9	29	10.0	7.9	8.4	30.8
		7	10.8	7.7	13.7	20.1	19	7.2	5.5	5.3	17.2
<i>Inga cocleensis</i>	Fabaceae	145	3.0	4.0	1.8	19.3	33	8.2	8.0	5.7	32.0
		133	4.3	5.3	2.0	27.3	27	4.7	4.4	3.7	14.7
<i>Inga marginata</i>	Fabaceae	540	2.1	4.0	1.2	26.8	51	8.5	8.6	6.6	32.1
		390	2.7	4.5	1.0	34.3	58	10.1	8.7	8.1	30.1
<i>Inga punctata</i>	Fabaceae	9	7.3	8.8	3.7	29.3	6	6.9	7.8	3.7	18.9
		8	5.9	4.8	6.1	12.3	5	8.7	9.5	7.3	24.2
<i>Inga spectabilis</i>	Fabaceae	9	3.1	3.3	1.8	8.9	11	5.9	4.8	5.5	17.4
		11	4.9	4.2	2.5	12.0	11	5.4	4.3	4.1	12.4
<i>Jacaranda copaia</i>	Bignoniaceae	91	4.9	6.1	2.3	28.0	209	13.0	13.2	11.2	59.7
		73	6.2	7.0	3.0	31.9	211	7.8	6.6	6.7	33.0

<i>Laetia procera</i>	Flacourtiaceae	11	6.4	4.4	7.2	13.3	8	7.1	10.7	5.5	27.4
		12	3.5	2.6	3.3	8.9	9	4.7	4.0	3.1	12.6
<i>Lafoensia punicifolia</i>	Lythraceae	4	3.9	1.9	4.1	5.7	3	9.8	8.9	4.9	20.0
		2	10.7	1.3	10.7	11.7	4	4.5	5.3	4.1	11.2
<i>Ochroma pyramidale</i>	Bombacaceae	1	60.6	0.0	60.6	60.6	3	44.8	30.3	48.1	73.4
		1	28.9	0.0	28.9	28.9	5	20.4	7.6	22.6	26.3
<i>Ocotea oblonga</i>	Lauraceae	112	2.1	2.7	1.2	12.2	26	10.4	14.8	7.7	71.1
		77	3.0	4.3	1.5	27.2	19	6.9	7.1	5.8	23.1
<i>Ocotea puberula</i>	Lauraceae	183	1.8	3.0	1.2	23.2	9	13.3	10.9	10.0	39.0
		152	2.0	3.6	0.9	35.0	9	12.2	10.3	8.3	30.9
<i>Pourouma guianensis</i>	Moraceae	28	2.7	3.6	1.9	12.9	11	8.6	6.8	6.3	23.9
		28	4.0	4.0	2.9	17.6	10	6.1	3.7	5.3	11.2
<i>Pseudobombax septenatum</i>	Bombacaceae	6	1.3	1.4	1.2	3.8	7	0.5	26.8	1.0	41.5
		1	3.8	0.0	3.8	3.8	7	9.8	6.7	11.2	19.2
<i>Simarouba amara</i>	Simaroubaceae	798	2.5	3.2	1.7	31.7	217	9.4	8.7	7.0	47.7
		714	2.8	3.3	1.9	21.3	204	6.7	5.1	5.9	22.5
<i>Solanum hayesii</i>	Solanaceae	42	4.7	5.0	2.4	20.1	21	6.1	12.1	2.3	55.9
		21	4.8	5.6	2.8	20.1	8	3.6	3.6	2.5	11.8
<i>Spondias mombin</i>	Anacardiaceae	26	5.5	5.8	3.0	22.8	20	12.9	11.4	11.3	46.2
		29	6.6	7.2	4.8	30.9	22	4.6	8.4	3.2	18.0
<i>Trema micrantha</i>	Ulmaceae	3	14.6	13.2	9.0	29.7	16	22.7	20.7	16.2	74.8
		3	28.1	18.5	25.9	47.6	6	16.3	6.4	17.2	24.4
<i>Turpinia occidentalis</i>	Staphyleaceae	61	3.3	3.6	2.0	16.4	49	5.0	5.9	4.0	21.1
		37	4.9	3.8	4.2	15.0	46	3.5	5.5	2.5	19.0
<i>Vochysia ferruginea</i>	Vochysiaceae	20	4.5	7.8	1.7	30.4	9	17.3	12.1	14.1	40.0
		15	4.4	4.9	2.1	15.3	9	13.4	6.9	12.5	22.1
<i>Zanthoxylum belizense</i>	Rutaceae	71	12.4	8.7	11.4	30.3	90	15.4	11.7	14.1	63.5
		68	13.8	9.9	12.0	38.1	88	9.8	8.5	8.7	33.4

For each species, the first row of data is for 1982-1985, the second for 1985-1990. n is the number of stems on which the estimates were based, and the mean, standard deviation, median, and maximum growth rates (in mm year⁻¹) are listed for two size classes. Growth rates above 75 mm year⁻¹ and all records showing decrements in dbh of more than 5% year⁻¹ were eliminated before calculating statistics.

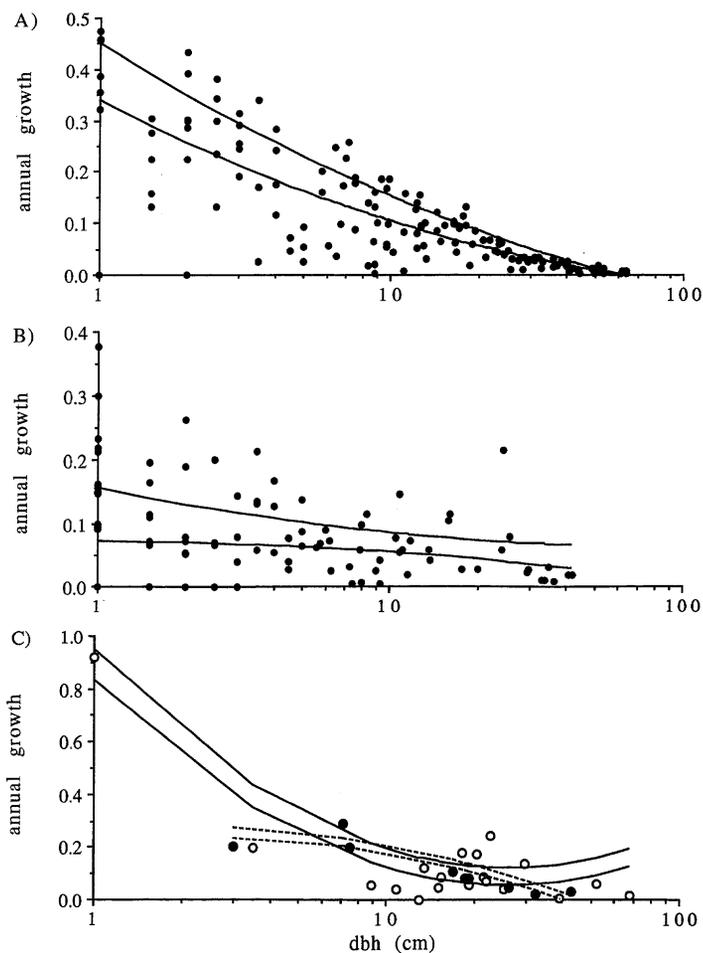


Fig. 5. Samples of fitted growth curves from three species. Each point represents growth rate of a single stem during one census interval. The lower curve in each figure is the quadratic regression fit to the data. The upper curve is the quadratic regression fit to the residuals above the mean (see text). (A) *Zanthoxylum belizense*, 1985–1990 data. (B) *Ocotea oblonga*, 1982–1985 data. The points on the horizontal axis represent multiple records; for example, 18 trees had dbh 1 and growth 0.0, and 14 had dbh 1.5 and growth 0.0. This is why the regression curve is nearly flat and the r^2 near zero. (C) *Trema micrantha*; 1982–1985 data shown by open circles and solid lines, 1985–1990 data by closed circles and dashed lines.

rates as judged by trajectories in Table 1 were in reasonable accord with raw growth rates as given in Table 2.

Error checking

For species with moderate sample sizes, we did not check all individual

records because one or two invalid estimates would not alter estimates much. For example, in *Zanthoxylum*, the fastest-growing stem above 30 cm dbh was an invalid record: its dbh in three censuses was recorded at 36, then 60, then 38 cm. However, removing it changed the regression parameters by less than 2%.

For species with smaller sample sizes, however, one or a few invalid estimates could lead to highly aberrant results. Indeed, we deleted one species from the list of top ranks after checking individual records. This was *Tetra-thylacium johansenii*, a tree that often produces sprouts at the base of the trunk that can make dbh estimates problematic. All eight trees above 40 cm dbh in this species had measurement problems; for example, one was recorded at 47, 36, then 48 cm in consecutive censuses, another at 42, 52, then 37 cm. Its rapid growth was entirely an artifact.

The other fast-growing species which had small samples, however, proved to have valid dbh measures that justified their growth estimates. All *Ochroma* stems grew rapidly: one was 4 cm in 1982, 20 cm in 1985, then 34 cm in 1990, and another was 14, 28, then 40 cm. In *Cavanillesia*, among stems of less than 50 cm dbh there were several seemingly valid estimates of rapid growth: one stem was 6 cm, 16 cm, then 24 cm in the three censuses, and one was 13, 20, then 34 cm. Likewise, *Trema* had many valid records of fast growth: for example, one stem was 30, 43, then 51 cm and one was 15, 19, then 30 cm. Most remarkably, one *Trema* stem was less than 1 cm (not included in the census) in 1982, 7 cm in 1985, then 32 cm in 1990; this was the most extreme increase in dbh we noted over the 8 year census period.

Discussion

The large dataset from the 50 ha mapped plot in Panama has allowed us to estimate growth rates for 160 species of trees. We used a straightforward technique for collapsing estimates of dbh increment into a single growth trajectory for each species, and from this identified the 28 fastest-growing species in the 50 ha plot. Although a few problems appeared in the data analysis, including erroneous dbh measures and faulty curve fits, on balance the technique gave reliable predictions about lifetime growth histories of a substantial number of tropical tree species. Few research programs have developed growth estimates for anywhere near 160 species of tropical trees, let alone in only 8 years.

At the fastest growth rates we documented, a handful of species reached 10 cm dbh in 5–12 years, 30 cm dbh in 15–25 years, and 60 cm in 30–45 years. These figures do not match growth of some plantation species, such as *Gmelina arborea*, *Leucaena* spp., *Acacia* spp., or *Pinus caribaea*, which can maintain growth of 3–5 cm year⁻¹ (C.A. Gomez et al., unpublished work, 1987; Hechavarría and Mercadet, 1988; MacDicken and Brewbaker, 1988; Hugh-

ell, 1991; Panitz and Yaacob, 1992), but growth of the few fastest individuals of *Ochroma* and *Trema* in the plot approached these rates. Of course, we anticipate that the tree species we analyzed would perform better in plantation than in forest, and some data bear this out. *Vochysia ferruginea* grew initially at 24 mm year⁻¹ in dbh and *Cordia alliodora* at 50 mm year⁻¹ in plantations in Costa Rica (Heuvelodop et al., 1985; Espinoza and Butterfield, 1992); both figures are much higher than those we documented at small sizes in the 50 ha plot. On the other hand, *Guazuma ulmifolia* grew no better in plantations than it did in the forest: 2–4 mm year⁻¹ in smaller trees (Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), 1986).

Not surprisingly, many of the fast-growing trees we identified are pioneer species. Indeed, 10 of the 28 species shown in Table 1 are common roadside trees of the region (*Annona*, *Apeiba*, both *Cecropia* species, *Cordia*, *Guazuma*, *Ochroma*, *Pseudobombax*, *Spondias*, and *Vochysia*). Welden et al. (1991) published an index of 'pioneerness' in the 50 ha plot—the fraction of recruits in light gaps—and this can be used as an objective assessment of the pioneer status of the species we identified. Welden et al. (1991) gave an index for 12 of the 28 species listed in Table 1. Seven had indices above 50, indicating recruitment strongly biased toward light gaps (both *Cecropia* species, *Cordia*, *Inga cocleensis*, *Jacaranda*, *Spondias*, and *Zanthoxylum*), one had a moderately high index of 33 (*Solanum*), but four species had indices close to the mean for the whole plot (both *Ocotea* species, *Inga marginata*, and *Simarouba*). Interestingly, these last four were among the species with slow growth early, but rapidly accelerating growth trajectories as they aged, confirming the notion that these are not pioneer species, as pioneers, by definition, have rapid early growth.

Some of the species listed in Table 1 have already been recognized for their rapid growth and tested in plantation. The balsa (*Ochroma*) was once studied in considerable detail because of its commercial value (Fletcher, 1951), and its rapid growth has been the subject of much attention (Whitmore and Gong, 1983). Espinoza and Butterfield (1992) worked with *Vochysia* in plantations; *Cordia* is one of the few native trees widely planted in plantations in Latin America (Heuvelodop et al., 1985; Nichols and González, 1991); *Guazuma*, *Inga spectabilis*, and *Jacaranda* have received attention from forestry agencies (Hornick et al., 1984; CATIE, 1986; Nichols and González, 1991). Richards (1952) noted examples of rapid growth in *Ceiba pentandra*.

Many of the species in Table 1, however, have not yet been recognized for their rapid growth and have not received attention in management circles. Of particular interest are the *Ocotea* species, which perform well at larger sizes and which have a congener with considerable timber value (the greenheart, *Ocotea rodiaei*, Fanshawe, 1948; Ter Steege, 1990). *Zanthoxylum*, *Trema*, *Hampea*, *Lafoensia*, *Pourouma*, and *Turpinia* are rapidly growing species

which, at least to our knowledge, have not been tested in reforestation trials. These species all warrant further consideration for their potential in attempts to reforest degraded soils.

One reason for the very high mean growth rates in these species may be that their stems occur only in open areas, under optimum light. For example, the few *Ochroma* stems in the 50 ha plot probably achieved such extraordinarily high mean growth simply because they are all in large canopy gaps; stems in shade do not survive. Many shade-tolerant species are probably capable of rapid growth, but their mean growth rates are low because most stems are in the shade. Condit et al. (1993) showed high variation in growth rates for one shade-tolerant species in the plot, *Prioria copaifera*. In fact, the maximum growth rates for *Prioria*, which were 20–40 mm year⁻¹, matched those for many species shown in Table 2 (but not the very fastest, such as *Ochroma* and *Trema*), and Ashton and Hall (1993) found in some Malaysian forests a guild of emergent, climax species capable of very rapid growth. Thus, there may be other species in the 50 ha plot that would respond with excellent growth in managed settings.

Our goal has been to identify a number of species with demonstrably high growth rates. Further experimentation with these species should be carried out to determine their economic and ecological value to forest managers. We recommend that they be tested for their usefulness in plantation forestry and their ability to recoup degraded soils and initiate the regeneration of forest cover—tests that would not take much time or many resources (Espinoza and Butterfield, 1992). Of course, attention should not be restricted to the fastest-growing species; other species may prove valuable as well. In certain situations where rapid growth is at a premium, however, it would be highly advisable to begin by testing species with proven growth records.

Acknowledgments

The Smithsonian Tropical Research Institute in Panama provided generous logistical and financial support for the censuses. We also thank the field workers—more than 100 people from 10 countries—who contributed to the censuses on BCI. The project has been supported by grants from the National Science Foundation, the Smithsonian Scholarly Studies Program, the Smithsonian Tropical Research Institute, the John D. and Catherine T. MacArthur Foundation, the World Wildlife Fund, the Earthwatch Center for Field Studies, the Geraldine R. Dodge Foundation, and the Alton Jones Foundation. This paper is a scientific contribution from the Center for Tropical Forest Science, which is supported by the John D. and Catherine T. MacArthur Foundation.

References

- Ashton, P.S. and Hall, P., 1993. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *J. Ecol.*, 80: 459–481.
- Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), 1986. Silvicultura de especies promisorios para producción de leña en América Central: resultados de cinco años de investigación. Informe técnico, CATIE, Turrialba, Costa Rica, No. 86, 228 pp.
- Condit, R., Hubbell, S.P. and Foster, R.B., 1992a. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *Am. Nat.*, 140: 261–286.
- Condit, R., Hubbell, S.P. and Foster, R.B., 1992b. Stability and change of a neotropical moist forest over a decade. *Bioscience*, 42: 822–828.
- Condit, R., Hubbell, S.P. and Foster, R.B., 1993. Mortality and growth of a commercial hardwood, 'el cativo', *Prioria copaifera*, in Panama. *For. Ecol. Manage.*, 62: 107–122.
- Croat, T.R., 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, CA, 943 pp.
- Del Valle, A.J.I., 1979. Curva preliminar de crecimiento del cativo (*Prioria copaifera*) en bosque virgen empleando el método de los tiempos de paso. *Rev. Fac. Nal. Agron. Colombia*, 32: 19–26.
- Duke, J.A., 1968. Darien Ethnobotanical Dictionary. Batelle Memorial Institute, Columbus, OH, 131 pp.
- Espinoza, C.M. and Butterfield, R., 1992. Adaptabilidad de 13 especies nativas maderables bajo condiciones de plantación en las tierras bajas húmedas del Atlántico, Costa Rica. In: R. Salazar (Editor), Manejo y aprovechamiento de plantaciones forestales con especies de uso múltiple. Actas Reunión IUFRO, Guatemala, 3–7 April 1989. CATIE, Turrialba, Costa Rica.
- Fanshawe, D.B., 1948. Studies of the trees of British Guiana. II. Greenheart (*Ocotea rodiaei*). *Trop. Woods*, 92: 25–40.
- Fletcher, M.I., 1951. Balsa—production and utilization. *Econ. Bot.*, 5: 107–125.
- García Colmenarez, J.R., 1978. Evaluación preliminar de la plantación experimental con especies forestales en las sabanas de la Estación El Irel Barrancas, Estado Barinas, Venezuela. *Rev. For. Venez.*, 28: 97–143.
- González, J., Butterfield, R., Segleau, J. and Espinoza C.M. (Editors), 1990. Primer encuentro regional sobre especies forestales nativas de la zona norte y atlántica. Memoria de 28–29 de julio, 1989, Organización para Estudios Tropicales y Dirección General Forestal. Instituto Tecnología de Costa Rica, Cartago.
- Hechavarría, O. and Mercadet, A., 1988. Comportamiento de tres procedencias de *Gmelina arborea* a los tres años de edad en Sierra del Rosario, Cuba. *Rev. For. Baracoa*, 18: 31–40.
- Heuvelink, J., Alpizar, L., Fassbender, H.W., Enriquez, G. and Folster, H., 1985. Sistemas agroforestales de café (*Coffea arabica*) con laurel (*Cordia alliodora*) y café con poró (*Erythrina poeppigiana*) en Turrialba, Costa Rica. II. Producción agrícola, maderable y de residuos vegetales. *Turrialba*, 35: 347–355.
- Hornick, J.R., Zerbe, J.I. and Whitmore, J.L., 1984. Jari's successes. *J. For.*, 82: 663–667.
- Hubbell, S.P. and Foster, R.B., 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. In: S.L. Sutton, T.C. Whitmore and A.C. Chadwick (Editors), *Tropical Rain Forest: Ecology and Management*. Blackwell Scientific, Oxford, pp. 25–41.
- Hubbell, S.P. and Foster, R.B., 1986a. Biology, chance, and the history and structure of tropical rain forest tree communities. In: J. Diamond and T.J. Case (Editors), *Community Ecology*. Harper and Row, New York, pp. 314–329.
- Hubbell, S.P. and Foster, R.B., 1986b. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In: M. Soulé (Editor), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer, Sunderland, MA, pp. 205–231.
- Hubbell, S.P. and Foster, R.B., 1990a. Structure, dynamics, and equilibrium status of old-growth

- forest on Barro Colorado Island. In: A. Gentry (Editor), Four Neotropical Rain Forests. Yale University Press, New Haven, CT, pp. 522–541.
- Hubbell, S.P. and Foster, R.B., 1990b. The fate of juvenile trees in a neotropical forest: implications for the natural maintenance of tropical tree diversity. In: M. Hadley and K.S. Bawa (Editors), Reproductive Ecology of Tropical Forest Plants. Man and the Biosphere Series, Vol. 7. UNESCO/IUBS, Paris and Parthenon, Carnforth, UK, pp. 325–349.
- Hubbell, S.P. and Foster, R.B., 1992. Short-term population dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. *Oikos*, 63: 48–61.
- Hughell, D., 1991. Modelo preliminar para la predicción del rendimiento de *Gmelina arborea* Roxb. en América Central. *Silvoenergía* (Costa Rica), No. 44.
- Instituto Nacional de Recursos Naturales Renovables (INRENARE), 1990. Plan de Acción Forestal de Panamá.
- Leigh, Jr., E.G., Rand, S.A. and Windsor, D.M. (Editors), 1982. The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes. Smithsonian Institution Press, Washington, DC, 468 pp.
- Lieberman, M. and Lieberman, D., 1986. Simulations of growth curves from periodic increment data. *Ecology*, 66: 632–635.
- MacDicken, K.G. and Brewbaker, J.L., 1988. Growth rates of five tropical leguminous fuelwood species. *J. Trop. For. Sci.*, 1: 83–91.
- Manokaran, N., LaFrankie, J.V., Kochummen, K.M., Quah, E.S., Klahn, J., Ashton, P.S. and Hubbell, S.P., 1990. Methodology for the 50-hectare research plot at Pasoh Forest Reserve. Research Pamphlet 104. Forest Research Institute of Malaysia, Kepong, 69 pp.
- Nichols, D. and González, E. (Editors), 1991. Especies nativas y exóticas para la reforestación en la zona sur de Costa Rica. Memoria II de 12–14 de febrero, 1989, Organización para Estudios Tropicales y Dirección General Forestal, organizadores. Oficina de Publicaciones de la UNED, San José, Costa Rica, 73 pp.
- Panitz, E. and Yaacob, A., 1992. Growth of *Acacia mangium* planted on windrow sites. *J. Trop. For. Sci.*, 4: 257–265.
- Purcell, E.J., 1972. Calculus with Analytic Geometry. Appleton–Century–Crofts, New York, 989 pp.
- Richards, P.W., 1952. The Tropical Rain Forest. Cambridge University Press, Cambridge, 450 pp.
- Saw, L.G., LaFrankie, J.V., Kochummen, K.M. and Yap, S.K., 1991. Fruit trees in a Malaysian rain forest. *Econ. Bot.*, 45: 120–136.
- Ter Steege, H., 1990. A Monograph of Wallaba, Mora and Greenheart. The Tropenbos Foundation, Ede, Netherlands, 141 pp.
- Torres de Araúz, R., 1975. Darién: Etnoecología de una Región Histórica. Dirección Nacional del Patrimonio Histórico, Instituto Nacional de Cultura, Panamá, 377 pp.
- Uhl, C., 1982. Recovery following disturbances of different intensities in the Amazon rain forest of Venezuela. *Interciencia*, 7: 19–24.
- Uhl, C., Jordan, C., Clark, K., Clark, H. and Herrera, R., 1982. Ecosystem recovery after cutting, cutting and burning, and bulldozer clearing treatments. *Oikos*, 38: 313–320.
- Welden, C.W., Hewett, S.W., Hubbell, S.P. and Foster, R.B., 1991. Survival, growth, and recruitment of saplings in canopy gaps and forest understory on Barro Colorado Island, Panama. *Ecology*, 72: 35–50.
- Whitmore, T.C., 1984. Tropical Rain Forests of the Far East. Clarendon Press, Oxford, 352 pp.
- Whitmore, T.C. and Gong, W.-K., 1983. Growth analysis of the seedlings of balsa, *Ochroma lagopus*. *New Phytol.*, 95: 305–311.

Submission of manuscripts.

The preferred medium of submission is on disk with accompanying manuscript (see "Electronic manuscripts" below). Manuscripts should be submitted in triplicate with the disk. Authors from the Americas, Australia, New Zealand and the Pacific are requested to send their manuscripts to *Forest Ecology and Management*, Dr. Richard F. Fisher, Department of Forest Science, Texas A&M University, College Station, TX77843-2135, USA; all other authors are requested to send their manuscripts to the Editorial Office, *Forest Ecology and Management*, P.O. Box 181, 1000 AD Amsterdam, The Netherlands.

Authors in Japan please note: if you would like information about how to have the English of your paper checked, corrected and improved (*before submission*), please contact our Tokyo office who will inform you of the services provided by language correctors: Elsevier Science Publishers (Japan), 20-12 Yushima 3-chome, Bunkyo-ku, Tokyo 113; tel. (03)-3833-3821; fax (03)-3836-3064.

All questions arising after acceptance of the manuscript, especially those relating to proofs, should be directed to Elsevier Editorial Services, Mayfield House, 256 Banbury Road, Oxford OX2 7DH, UK, tel. (+44-865) 54252, fax (+44-865) 516120 or 56472.

Electronic manuscripts: Electronic manuscripts have the advantage that there is no need for the rekeying of text, thereby avoiding the possibility of introducing errors and resulting in reliable and fast delivery of proofs. The preferred storage medium is a 5¼ or 3½ inch disk in MS-DOS format, although other systems are welcome, e.g., Macintosh (in this case, save your file in the usual manner, do not use the option 'save in MS-DOS format'); if you use NEC, please submit your article on a double density or high density 5¼ inch disk or double density 3½ inch disk (**not** a high density 3½ inch disk). Please **do not split** the article into separate files (title page as one file, text as another, etc.). Ensure that the letter 'l' and digit '1' (also letter 'O' and digit '0') have been used properly, and structure your article (tabs, indents, etc.) consistently. Characters not available on your wordprocessor (Greek letters, mathematical symbols, etc.) should not be left open but indicated by a unique code (e.g. α , @, #, etc., for the Greek letter α). Such codes should be used consistently throughout the entire text. Please make a list of such codes and provide a key. Do not allow your wordprocessor to introduce word splits and do not use a 'justified' layout. Please adhere strictly to the general instructions on style/arrangement and, in particular, the reference style of the journal. It is very important that you save your file in the wordprocessor format. If your wordprocessor features the option to save files "in flat ASCII", please **do not** use it. Format your disk correctly and ensure that only the relevant file (one complete article only) is on the disk. Also, specify the type of computer and wordprocessing package used and label the disk with your name and the name of the file on the disk. After **final acceptance**, your disk plus one, final, printed and exactly matching version (as a printout) should be submitted together to the accepting editor. **It is important that the file on disk and the printout are identical.** Both will then be forwarded by the editor to Elsevier. Further information may be obtained from the Publisher.

Advertising information: Advertising orders and enquiries may be sent to: Elsevier Science Publishers B.V., Advertising Department, P.O. Box 211, 1000 AE Amsterdam, The Netherlands, tel. (+31-20) 5153220, fax (+31-20) 6833041. In the UK: TG Scott & Son Ltd., attn. Tim Blake/Vanessa Bird, Portland House, 21 Narborough Rd., Cosby, Leicestershire, LE9 5TA, UK, tel. (0533) 753333, fax (0533) 750522. In the USA and Canada: Weston Media Associates, attn. Daniel Lipner, P.O. Box 1110, Greens Farms, CT 06436-1110, USA, tel. (203) 2612500, fax (203) 2610101.

***Forest Ecology and Management* has no page charges**

For a full and complete Guide for Authors, please refer to pages 361–365 of this issue.

© 1993, Elsevier Science Publishers B.V. All rights reserved.

0378-1127/93/\$06.00

No part of this publication may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, without the prior written permission of the publisher, Elsevier Science Publishers B.V., Copyright and Permissions Department, P.O. Box 521, 1000 AM Amsterdam, The Netherlands.

No responsibility is assumed by the Publisher for any injury and/or damage to persons or property as a matter of products liability, negligence or otherwise, or from any use or operation of any methods, products, instructions or ideas contained in the material herein.

Although all advertising material is expected to conform to ethical (medical) standards, inclusion in this publication does not constitute a guarantee or endorsement of the quality or value of such product or of the claims made of it by its manufacturer.

This journal is printed on acid-free paper.

Printed in The Netherlands