

## ASSESSING THE GROWTH OF TROPICAL RAIN FOREST TREES: ISSUES FOR FOREST MODELING AND MANAGEMENT

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**Abstract.** Growth performance was assessed for a diverse suite of canopy and emergent tree species in a lowland neotropical rain forest (the La Selva Biological Station, north-eastern Costa Rica). Species were evaluated based on annual diameter measurements of large samples of individuals in all post-seedling size classes, over a 12-yr period. The study species were seven non-pioneers (*Minuartia guianensis*, *Lecythis ampla*, *Hymenolobium mesoamericanum*, *Simarouba amara*, *Dipteryx panamensis*, *Pithecellobium elegans*, and *Hyeronima alchorneoides*) and two pioneers (*Cecropia obtusifolia* and *C. insignis*). For each species, inherent growth capacity through ontogeny was estimated as the mean of the five largest annual increments (from different individuals) in each juvenile and adult size class. At all tree sizes, species differed highly significantly in this measure. In the small sapling sizes ( $\leq 4$ -cm diameter), the two pioneers showed markedly higher maximum growth than all the non-pioneers, in line with current understanding. This growth advantage, however, was quickly lost with increasing tree size. For eight of the nine species, the ontogenetic patterns of maximal growth closely corresponded to species groupings previously based on juvenile microsites (forest stage, light levels). Average growth rates, however, which are the combined result of environmental and biotic factors, did not show this correspondence. The groups based on microsite occupancy and growth potential provide a starting point for treating the great numbers of species of tropical rain forest trees as many fewer functional types, a sine qua non for modeling these complex forests. The exceptional growth capacity of one of our focal non-pioneer species (*Simarouba*) suggests that it represents a hitherto unrecognized functional type among tropical rain forest trees.

The data from this long-term study indicate that several assumptions of current forest-dynamics models are not applicable to trees of this biome. For most species (1) diameter growth during regeneration was not correlated with tree size; (2) adult sizes were not characterized by a constant maximal basal-area increment; and (3) growth capacity did not decline toward zero as trees approached maximum size. Evaluation of overall increment distributions revealed a broad adult size range of exclusively high growth in the emergent *Hymenolobium*; for two additional species, sectors of the adult size range showed an absence of very low or negative growth. At most sizes, however, all nine species displayed the full range of growth increments, from slightly negative to observed maxima. Describing the performance of tropical rain forest canopy trees will require similar analysis of growth data obtained from many individuals and intervals, and stratified across juvenile and adult life stages. More realistic forest-dynamics models will depend on such evaluations of many tree species, in diverse tropical rain forests. Such models are greatly needed, both for designing management for this biome and for predicting its responses to changing climate and atmospheric conditions.

**Key words:** *Cecropia*; forest-dynamics models; forest management; growth capacity; growth, inherent vs. average; La Selva Biological Station, Costa Rica; ontogenetic switching; pioneer species; tree growth; trees, functional groups for use in models; tropical rain forest.

### INTRODUCTION

Major current challenges for ecologists are to understand and to be able to predict the dynamics and productivity of the world's tropical rain forests. Tropical evergreen forests are disproportionately important in the world's carbon budget. Only 14% of vegetation

by area, they are estimated to account for 36% of terrestrial net primary production (NPP) (Melillo et al. 1993). There is very incomplete knowledge of the carbon stores and fluxes in these ecosystems and of their responses to and potential effects on the changing world climate and atmospheric composition (cf. Körner 1995a, Schimel 1995). Long-term strategies for forest management will also require a better process-level understanding.

Developing realistic forest-dynamics models for this biome is therefore a standing research need. To do this will require collapsing the great numbers of tree species

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in any tropical wet or moist forest into a much smaller set of tree types, or functional groups (cf. Vanclay 1991, Körner 1993). Towards this end, tree growth in these forests has to be assessed and then modeled. How diverse are the growth characteristics of tropical rain forest trees? Inherent growth potential of the trees in a forest, i.e., their maximum growth under the conditions of that site, is the theoretical basis for most forest-dynamics models. How does inherent growth potential vary among tropical tree species? Does this significantly change with ontogeny (Oldeman and van Dijk 1991, Grubb 1996), or can a given species be adequately characterized by a single growth function? Are the growth characteristics of tropical trees consonant with major assumptions of the growth modules in current forest-dynamics models? Does species-level variation in tree growth patterns have important impacts on system-wide processes such as net primary production? To answer these questions will take considerably more data than are currently in hand (Vanclay et al. 1997).

The obstacles to a better understanding of tree growth in this biome are daunting. For most tropical rain forest (TRF) sites, descriptive floristics of the trees are grossly incomplete, and progress toward complete inventories is hampered by undercollecting, difficult access and logistics, and the fluid nature of tropical-tree systematics (see Gentry 1994). In the few cases where such inventories have been carried out in TRF, the diversity of trees  $\geq 10$  cm diameter is typically found to be 80–300+ species/ha (cf. Lieberman et al. 1985*b*, Foster and Hubbell 1990, Gentry 1992, Valencia et al. 1994). An important corollary to this high diversity is that most of the tree species are locally rare (cf. Hubbell and Foster 1986*a*, Kochummen et al. 1990, Lieberman and Lieberman 1994). As a result, most published data on tree growth in TRF have been restricted to the small subset of species that provide modest to reasonable samples in study plots or transects (e.g., Lieberman et al. 1985*a, b* [most abundant 17% of species]; Korning and Balslev 1994 [most abundant 4% of species]).

Even for those species that have been studied, the growth data are limited. Reliable annual growth rings are not produced by TRF trees (Bormann and Berlyn 1981), except in the special circumstances of annually flooded forest (Worbes et al. 1992). Therefore stem increments can only be assessed through repeat bole measurements. In most long-term studies of tree growth in TRF (e.g., Primack et al. 1985, all studies cited in Swaine and Lieberman 1987, Vanclay 1991, Ashton and Hall 1992, Condit et al. 1993*a, b*, 1996, Korning and Balslev 1994, Lieberman and Lieberman 1994), measurements have been from multiple-year periods. Supra-annual censuses make it difficult to assess a tree species' inherent growth potential in TRF, because climate variation among years (cf. Clark and Clark 1994) and gap dynamics (Hubbell and Foster 1986*b*, Denslow

1987) can cause an individual's growth to vary substantially within multiyear census intervals. Moreover, in most TRF tree-inventory plots (e.g., Primack et al. 1985, all studies cited in Swaine and Lieberman 1987, Vanclay 1991, Ashton and Hall 1992, Favrichon 1994, Korning and Balslev 1994), the smallest measured trees are 10 cm in diameter and are already in the subcanopy or canopy (important exceptions are the 50-ha plot studies [Condit 1995], with inventories down to 1-cm diameter). With a 10-cm diameter cutoff, no information is gathered on the species' earlier life-history stages, whose growth characteristics can greatly differ from those of larger trees. Additionally, in long-term or large-scale studies, quality control of the tree measurements can be difficult (Condit et al. 1993*a, b*, Vanclay 1994, Gourlet-Fleury and Montpied 1995) and the resulting errors can limit the uses of the data for interpreting tree growth characteristics. Finally, the same species can show greatly different growth performance among old-growth sites, logged forest, successional stands, and sites with contrasting soil fertility (cf. Schulz 1960, Primack et al. 1985, Favrichon 1994, Silva et al. 1995, ter Steege et al. 1995, Vandermeer et al. 1997). All these factors help explain why we are far from understanding the nature and diversity of tree growth patterns in tropical rain forests.

Our long-term studies of the population ecology of canopy trees in a lowland neotropical forest have provided us an exceptional opportunity for characterizing and comparing the growth characteristics of diverse tree species in old-growth TRF. The data analyzed in this paper consist of 12 yr of annual increments, for all life-history stages from 50-cm-tall saplings to the largest adults, of canopy and emergent tree species spanning a broad life-history spectrum (Clark and Clark 1992). Although most of our nine study species are locally rare, samples of all post-seedling size classes were obtained by locating individuals within 216 ha of old-growth forest.

We address here several questions about these TRF tree species. How does their growth vary ontogenetically? What is their inherent growth potential in old-growth forest conditions? What is the relation between this growth potential, based on maximum observed increments, and the more commonly assessed average growth? How do these species' growth characteristics relate to their contrasting patterns of microsite occupancy through regeneration? Is tree growth in this TRF consistent with several major assumptions of the growth modules of current forest-dynamics models? We then discuss the implications of our findings for defining functional groups of tropical trees and for modeling the dynamics and productivity of tropical rain forest.

## METHODS

### *Study site and species*

The 1550-ha La Selva Biological Station of the Organization for Tropical Studies (OTS) is in the Atlantic

TABLE 1. The nine study species under long-term study in old-growth tropical rain forest at the La Selva Biological Station, Costa Rica.

Microsite group†	Species‡	Stratum attained	Maximum bole diameter (cm)§	(No. of trees ≥30 cm in diam.)	Wood density (g/cm³)
A	<i>Miquartia guianensis</i> Aubl. (Olacaceae) [G. Herrera 2250]	Canopy	82	(115)	0.98
A	<i>Lecythis ampla</i> Miers (Lecythidaceae) [R. Robles 2208]	Emergent	161	(67)	0.68¶
B	<i>Hymenolobium mesoamericanum</i> H.C. Lima (Papilionoideae) [R. Aguilar 19]	Emergent	156	(34)	0.70–1.00#
B	<i>Dipteryx panamensis</i> (Pittier) Record & Mell (Papilionoideae) [R. Robles 1199]	Emergent	187	(140)	0.84¶
B	<i>Simarouba amara</i> Aubl. (Simaroubaceae) [R. Robles 1670]	Canopy	81	(47)	0.40–0.50# 0.38††
C	<i>Pithecellobium elegans</i> Ducke (Mimosoideae) [B. Hammel 17319]	Emergent	137	(198)	no data
C	<i>Hyeronima alchorneoides</i> Allemao (Euphorbiaceae) [Chacon 751]	Emergent	187	(98)	0.60–0.67††
D	<i>Cecropia insignis</i> Liebm. (Cecropiaceae) [W. Burger 11135]	Canopy	54	(21)	0.35–0.45#
D	<i>Cecropia obtusifolia</i> Bertol. (Cecropiaceae) [R. Robles 1446]	Subcanopy/Canopy	35	(10)	0.35–0.45#

Note: Voucher specimens are in the Herbario Nacional de Costa Rica, San José, Costa Rica (except for the voucher for *Hyeronima*, which is at the Instituto Nacional de Biodiversidad de Costa Rica, Santo Domingo de Heredia, Costa Rica).

† See Table 2 for explanation of groups.

‡ Family is in parentheses; voucher specimen is in brackets.

§ At La Selva; measured from above buttresses (basal bole expansions) (See *Methods: Annual stem-diameter measurements*).

|| Record and Mell 1924 (air-dry).

¶ King 1996 (oven-dry mass/green volume).

# Record and Hess 1949; genus-level data (air-dry).

†† Chudnoff 1984 (oven-dry mass/green volume).

lowlands of Costa Rica (10°26' N, 84°00' W; elevation 37–150 m). It is classified as tropical wet forest in the Holdridge life-zone system (Hartshorn and Hammel 1994). Mean annual rainfall is 3962 mm, and all months average at least 100 mm (Sanford et al. 1994). The flora include 339 tree species (Hartshorn and Hammel 1994, D. A. Clark and D. B. Clark, *unpublished data*). Although not subject to large-scale disturbances such as hurricanes, the forest is very dynamic. Stem turnover is high (2.0–2.3%/yr for trees ≥10 cm in diameter at breast height [dbh]; Lieberman et al. 1990), as is the frequency of gap formation (Hartshorn 1978, Sanford et al. 1986). La Selva's soils range from relatively fertile entisols and inceptisols to infertile ultisols (Vitousek and Denslow 1987, Sollins et al. 1994). A comprehensive site overview is given by McDade et al. (1994).

We used three criteria to select the study species (see Table 1 for names and characteristics of the nine species; in the text, all species but the *Cecropia*'s will be named by genus only). (1) We included emergents, trees whose mature crowns extend above the average canopy level. Because emergents experience an extreme microhabitat range through ontogeny, they may share ecological and physiological characteristics (Mooney et al. 1980, Bazzaz 1984) and thus constitute a well-defined tree "functional group." Due to their large stature, emergents can also greatly affect forest

structure and processes (Lugo and Brown 1992, Brown et al. 1995, Clark and Clark 1996). The population ecology of tropical emergents is poorly known, in part due to their frequently low densities (Foggie 1960, Knight 1975, Clark and Clark 1987, 1996). (2) In an attempt to sample over the entire potential gradient of tree life-history types, we included species that had been subjectively classified as contrasting in shade tolerance or gap-dependence. Our subsequent analyses of the microhabitats of different-sized juveniles at first encounter (Clark and Clark 1992) revealed four strongly contrasting patterns of microsite occupancy through regeneration for these nine species (Table 2). (3) We included timber trees of local or regional economic value (all but the two *Cecropia* spp.).

Six species (*Miquartia*, *Lecythis*, *Hymenolobium*, *Dipteryx*, *Pithecellobium*, and *Hyeronima*) have been under study since 1983. In 1988 we added three species commonly thought to be at the "gap/high-light" end of the life-history spectrum: *Cecropia insignis*, *C. obtusifolia*, and *Simarouba*. Because all nine species can flower by the time they reach diameters ≥30 cm in the La Selva old growth (D. B. Clark and D. A. Clark, *unpublished data*), we refer to trees this size as "adults," and we use the terms "saplings" and "juveniles" for smaller individuals (this division is arbitrary, however; especially in the two *Cecropia* spp., trees of <30-cm diameter may be reproductive).

TABLE 2. Four regeneration patterns (groups A–D) based on microsite characteristics, for nine canopy tree species in old-growth forest at La Selva, Costa Rica (based on findings reported in Clark and Clark [1992]).

Group	Regeneration pattern	Tree species
A	Trees associated with dark, non-gap microsites through regeneration.	<i>Minquartia</i> , <i>Lecythis</i>
B	Trees establish in dark, non-gap sites but, with increasing sapling size, trees increase in crown illumination and are increasingly biased toward gap/building microsites.	<i>Hymenolobium</i> , <i>Dipteryx</i> , <i>Simarouba</i>
C	Trees are strongly associated with gaps as small saplings and again as subcanopy trees, but survive well as intermediate-sized juveniles as the canopy closes.	<i>Hyeronima</i> , <i>Pithecellobium</i>
D	Trees are associated with gaps and/or higher crown illumination through all juvenile stages.	<i>Cecropia insignis</i> , <i>Cecropia obtusifolia</i>

#### Population samples and annual censuses

As in other tropical moist or wet forests, at La Selva most trees and lianas are rare (83% of 269 species in three 4-ha inventory plots had densities  $\leq 1$  plant/ha for stems  $\geq 10$  cm in diameter; Lieberman et al. 1985a, b). Certain juvenile size classes are also frequently scarce (e.g., 10–30 cm diameter *Dipteryx*, 0.25 trees/ha; Clark and Clark 1987). Analysis of performance in all life-history stages of most species thus cannot be based on tree inventory plots, although the 50-ha plots in several tropical sites (Condit 1995) greatly extend the proportion of species that can be studied.

To evaluate tree performance in all size classes and microhabitats, we used landscape-scale sampling. The methods (detailed in Clark and Clark 1992) were designed to accumulate samples of individuals from all post-seedling size classes, over a large area (216 ha of old growth, excluding swamps), and non-biased in terms of microsite or tree condition. All sampled individuals have been marked, mapped, and censused annually until death is confirmed in successive censuses. Trees are measured in the same sequence each year, during January–June, to maintain close to annual inter-census intervals and thereby control for any seasonal effects on growth (e.g., in 1994–1995 the re-measurement interval for 94% of the trees ( $n = 2011$ ) was  $365 \pm 16$  d). Data analysed in this paper are from the period 1983–1995.

#### Annual stem-diameter measurements

Protocols for diameter measurements depend on tree size. For individuals  $< 4$  cm in diameter, maximum stem diameter is measured with a calipers to the nearest 0.1 mm at a marked point of measurement (POM) be-

low the lowest branch and away from stem irregularities. We measure these small trees at the highest acceptable point among the following: at or close to the stem base, at 40 cm above the ground, or at 130 cm above the ground. Over time, the POM is moved upward. Double measurements are taken in years when the POM changes, to enable increment calculations from both the past and succeeding growth years. Boles  $\geq 4$  cm in diameter are measured with a diameter tape to the nearest millimeter, rounding down. The tape is passed under any vines or roots on the stem and then is moved back and forth to clean the POM of loose bark and debris. Boles are measured at 130 cm above the ground (“breast height”) when this point is not affected by buttresses (basal bole expansions) or major stem deformities; otherwise, the POM is above such irregularities, often 5–7 m above the ground. Each tree’s POM is marked by an aluminum nail 10 cm higher on the bole. In years when buttresses or other stem irregularities are found to have developed near the POM, it is moved up, and diameter is measured at both points. Annual diameter growth is calculated as the difference between successive annual diameter measurements at the same POM, divided by (days between measurements/365).

Quality control of the diameter data has been an ongoing priority. Only three experienced field technicians have measured diameters during the project. A calibration, based on re-measurement of the same 50–70 trees after a two-to-several day interval, is performed before each year’s census. The accuracy of diameter data averages  $\pm 0.3$  mm (Clark and Clark 1992). When each diameter measurement is taken, it is checked against the previous year’s diameter (on the field data forms), and the tree is re-measured in cases of large increases or decreases (and this is noted, along with any supporting observations). Data quality is also assessed by checking the master database for consistency of a tree’s measurements across years. In the few cases of clearly contradictory data (e.g., a large diameter loss or gain bracketed by years with nearly constant diameter), the inconsistent data are either corrected (when this can be done unambiguously) or eliminated (flagged as “no data”).

#### Crown illumination

The potential availability of light in each tree’s microhabitat is assessed annually with a crown illumination index (detailed in Clark and Clark 1992). This index, which scores the source and relative amount of crown exposure to direct light, was strongly correlated with potential light as estimated from hemispherical photographs taken over saplings at La Selva (Clark and Clark 1992). The index ranges from 5 (crown completely exposed to overhead and lateral light) to 1 (no direct light).

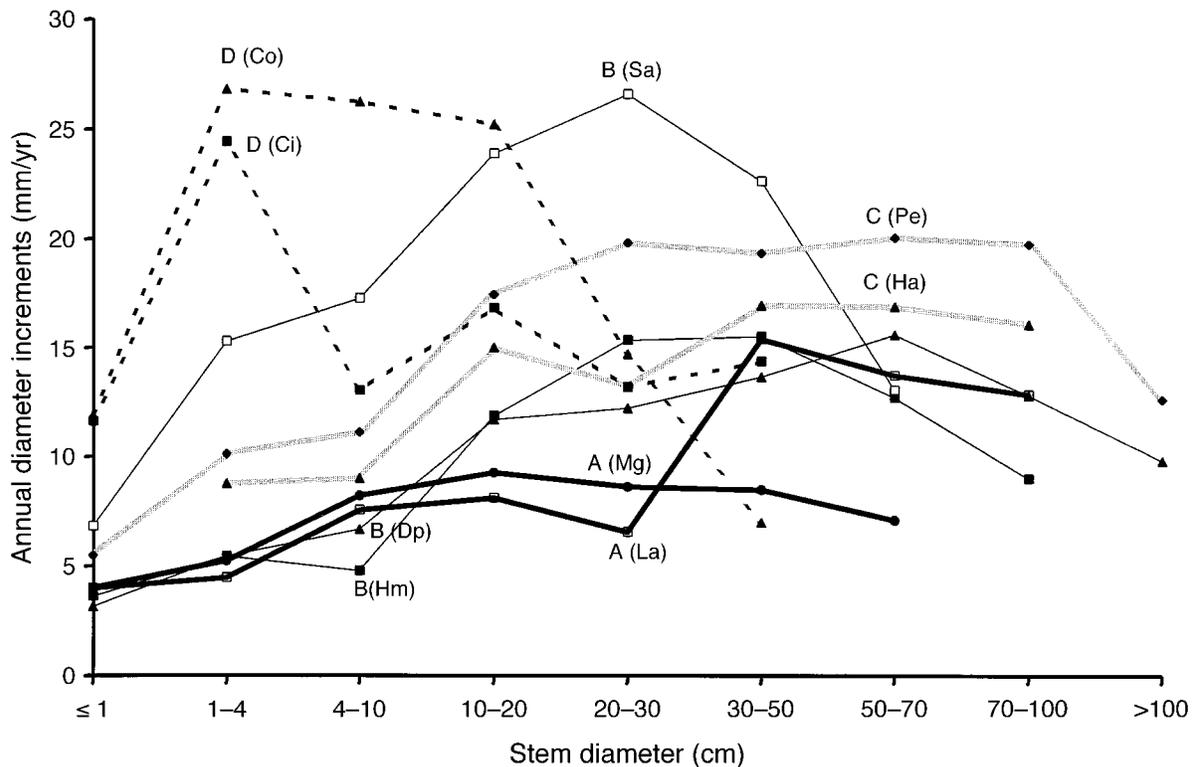


FIG. 1. Growth potential of the nine tropical rain forest tree species, based on the mean of the five maximum annual diameter increments in each size class. The five values from each species size class are from five different individuals. Sample sizes and statistical comparisons are given in the Appendix. Line labels (A–D) indicate the microsite group (see Table 2) and species initials: Ci = *Cecropia insignis*, Co = *C. obtusifolia*, Dp = *Dipteryx panamensis*, Ha = *Hyeronima alchorneoides*, Hm = *Hymenolobium mesoamericanum*, La = *Lecythis ampla*, Mg = *Miquartia guianensis*, Pe = *Pithecellobium elegans*, Sa = *Simarouba amara*. Line patterns are keyed to microsite groups: Group A = thick black; Group B = thin black; Group C = grey; Group D = dashed black.

## RESULTS

No single descriptor adequately characterizes the growth of any of these nine tropical rain forest (TRF) tree species. Interspecific rankings of the trees' growth rates differ substantially depending on the size range considered and on whether the ranking is based on maximum growth rates, average growth rates, or total increment distributions. Maximum growth rates, which indicate a species' inherent growth potential, are considerably more informative than averages. Patterns of maximum growth, but not average growth, correspond well with the species' patterns of juvenile microsite occupancy. Features of the growth of these TRF trees fail to support major assumptions of current forest-dynamics models.

### Maximum growth rates

The nine species show markedly differing patterns of inherent growth potential in old-growth forest (Fig. 1, Appendix). Growth potential at each size was estimated as the mean of the five largest annual diameter increments (constrained to be from five different trees, to allow statistical comparisons among species) observed during the 12-yr period. At all sizes the nine

species differ substantially in the mean of their maximum increments (Appendix).

The effect of the differing sample sizes on these estimates of growth potential appears to be conservative with respect to relative species ranks (Appendix). Within a size class, the largest sample sizes are associated with mean maximum increments that are among the lowest for that tree size. Similarly, the smallest sample sizes are associated with relatively high mean maximum increments. For saplings  $\leq 1$  cm in diameter, for example, the maximum diameter increments of three species with large sample sizes (*Miquartia*, 122 saplings; *Lecythis*, 76 saplings; *Dipteryx*, 134 saplings) all averaged  $\leq 4$  mm/yr. In contrast, maximum growth of the two *Cecropia* species at this size averaged 12 mm/yr, in spite of the small samples (13 and 17 saplings, respectively).

Eight of the nine species show patterns of potential growth as juveniles (maximum increments at diameters  $< 30$  cm; Fig. 1 and Appendix) that parallel their patterns of juvenile microsite occupancy (Table 2). The four species with the lowest potential juvenile growth rates are from microsite Groups A and B, those species characterized by large seeds and the ability to establish

small saplings in the understory. Of these, the two Group A species (*Minquartia* and *Lecythis*), those consistently associated with darker, non-gap microsites, have remarkably similar and notably low maximum increments as juveniles (trees <30 cm diameter). These species only very rarely grow 10 mm/yr or more in diameter over this size range (*Minquartia*: 2 out of 3371 total increments  $\geq 10$  mm/yr, namely, trees 13.6 and 25.9 cm in diameter; *Lecythis*: 1 out of 1905 total increments  $\geq 10$  mm/yr, i.e., a tree 19.7 cm in diameter). Microsite Group B species are characterized by ontogenetic increases in crown lighting and in the degree of association with gaps or building (intermediate, low-canopy) sites. Two of the three Group B species, *Hymenobium* and *Dipteryx*, have maximum diameter increments as low as those of Group A at small sapling sizes (to 10-cm diameter); however, once these species reach the subcanopy (diameters 10–<30 cm), their maximum growth averages >10 mm/yr. The Group C species, *Pithecellobium* and *Hyeronima*, are those strongly associated with gap/building sites as small saplings and again at 10–20 cm diameter. These two species show juvenile growth potentials that are intermediate between those of the low-growth A and B species and those of the two Group D species. The *Cecropias* of Group D had potential growth as small saplings ( $\leq 4$  cm in diameter) that greatly exceeded that of all the other seven species, in line with prevailing concepts of pioneers (cf. Swaine and Whitmore 1988). Taken together, these data show a marked correspondence between these species' four contrasting patterns of juvenile microsite distributions and the rankings of their potential growth rates as juveniles.

A notable exception, however, is *Simarouba*. Although it shows a Group B pattern of microsite occupancy (Table 2), *Simarouba*'s maximum diameter increments (Fig. 1, Appendix) overlap with or exceed those of the two *Cecropia* species (Group D) over much of the juvenile size range (4–30 cm diameter). Further, *Simarouba*'s growth potential (Fig. 1) contrasts strongly with that of the other two Group B species, which show only half *Simarouba*'s potential growth rate at most juvenile sizes (Appendix).

For all nine species, the patterns of potential diameter growth are highly size dependent (Fig. 1). These marked ontogenetic changes in growth capacity obviate any simple classification of these trees into "fast-growing" and "slow-growing" species. For example, the exceptionally high growth potential generally assumed to distinguish pioneers from non-pioneers (cf. Swaine and Whitmore 1988) is evident for the two *Cecropia* species only in the smaller juveniles. Once both *Cecropia*'s reach subcanopy sizes (20–30 cm diameter), their maximum growth rates in the La Selva old growth are statistically indistinguishable from those of all seven non-pioneer species (Appendix). Also notable are the relative growth rankings once these pioneer trees reach the canopy (at ~30-cm diameter at La Selva;

Clark and Clark 1992). At diameters of 30–50 cm, for example, *C. obtusifolia*'s maximum growth is significantly lower than that of three of the non-pioneer species (*Simarouba*, *Pithecellobium*, and *Hyeronima*; Appendix). All five emergent species show substantial maximum growth rates at all sizes above canopy level (9–23 mm/yr; Appendix). *Simarouba*'s pattern of growth potential (Fig. 1) is unique for the non-pioneers in showing a strong decline on reaching the canopy.

Neither juvenile potential growth rates nor juvenile microsite distributions are good indicators of potential growth rates of these species as adult trees ( $\geq 30$  cm in diameter). Although the relative ranks of their maximum diameter growth remain consistent through the juvenile sizes (Friedman two-way ANOVA, mean maximum increments of all nine species in four diameter classes [ $>1$ –4 cm,  $>4$ –10 cm,  $>10$ –20 cm,  $>20$ –<30 cm],  $P = 0.001$ ), there is no correlation between the relative ranks of these species' potential diameter growth as small juveniles (1–4 cm diameter) and as adults 30–50 cm in diameter (Spearman's  $R_s = 0.04$ ; Fig. 1). The emergent *Lecythis* exemplifies this ontogenetic switching. It shifts from being the species with the slowest potential growth in the subcanopy (maximum increments of only 6.5 mm/yr at  $>20$ –<30 cm diameter) to having notably high maximum diameter growth (13–15 mm/yr) at larger sizes (Appendix). In contrast, the other Group A species, the canopy tree *Minquartia*, shows relatively low maximum growth rates throughout its adult size range.

#### Average growth rates

The total distributions of diameter increments, and their central tendency, present a different picture of these species' growth characteristics from that shown by the potential (maximum) growth rates. As with the latter, however, the rankings of the overall increment distributions of the nine tree species are highly size dependent.

As small juveniles (to 4-cm diameter), the seven non-pioneer species show indistinguishable, and very low, diameter growth (Fig. 2) in the La Selva old-growth forest (93–100% of their annual increments were <5 mm). Evaluation of these species based solely on their average diameter increments as small saplings would indicate (1) that the seven non-pioneers have basically the same growth pattern, and (2) that this pattern contrasts strongly with that of the two pioneers (the *Cecropia* species, for which 36–46% of diameter increments were  $\geq 5$  mm/yr at these small sapling sizes).

As 4–10 cm diameter juveniles, again six of the seven non-pioneers show very similar slow growth overall (Fig. 2); however, in this size range *Simarouba*'s increment distribution is distinct from that of the other non-pioneers and in fact strongly overlaps those of the *Cecropia*'s. In the larger juvenile sizes ( $>10$ –<30 cm diameter), the three Group B species form a broad continuum of growth distributions that overlaps those of

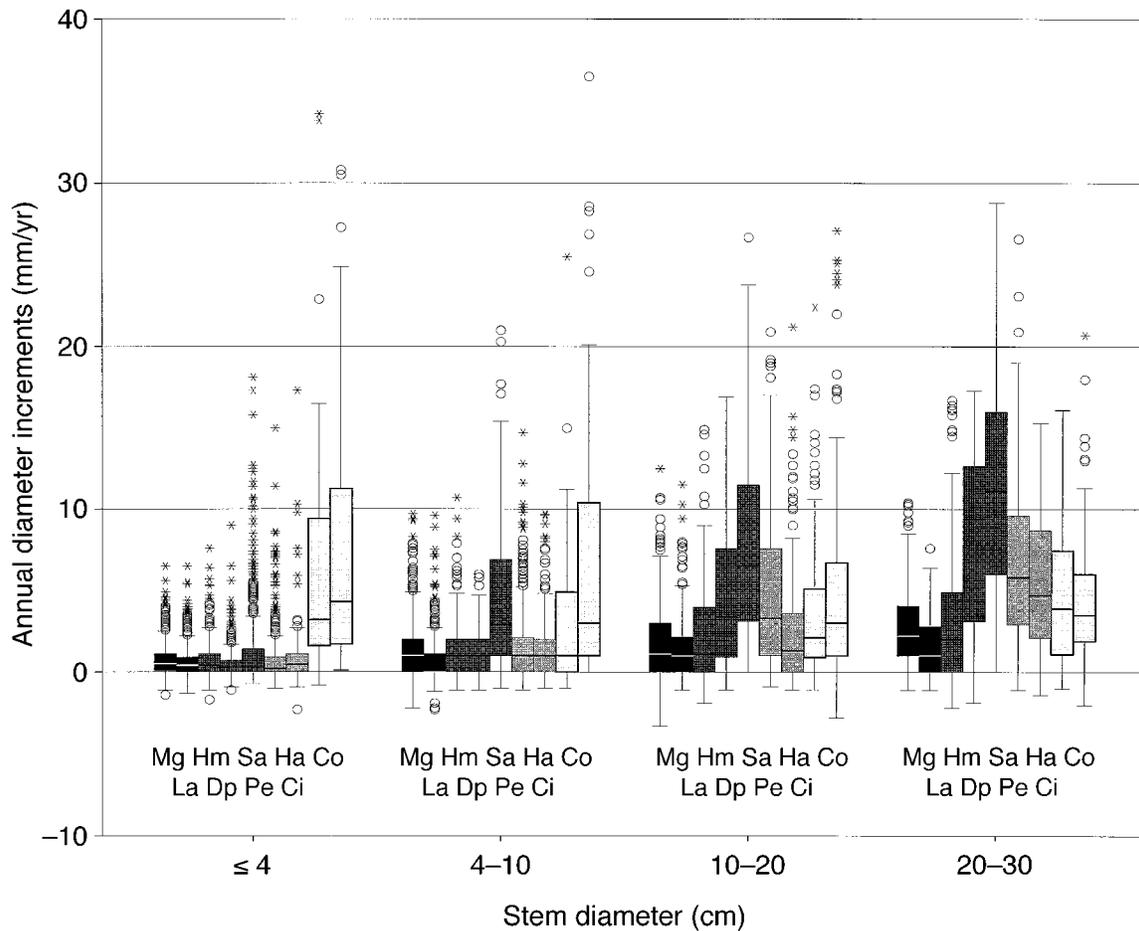


FIG. 2. Box plots of the total distributions of diameter increments, by juvenile size class. In each box, the center horizontal line indicates the median, and the two box halves enclose the upper and lower quartiles around the median. "Whisker" lines extend to the highest and lowest values that are not either "outliers" (circles: cases 1.5–3.0 box lengths from the box) or "extremes" (asterisks: cases >3 box lengths from the box). Species are labeled by initials (see Fig. 1 for key), and boxes are shaded to indicate microsite groups: black (Group A), successively lighter tones (Groups B, C, D).

all the other species, a pattern not displayed by their maximum growth rates (see above, *Maximum growth rates*). The progressive ontogenetic divergence between the overall juvenile increment distributions of the two Group B species *Hymenolobium* and *Dipteryx* contrasts markedly with their strong similarity in potential growth rates as juveniles (Fig. 1). Over the total range of juvenile sizes, only the two Group A species and *Hymenolobium* (Group B) maintain consistently low growth rates (Fig. 2). The other four non-pioneers show marked size-related changes in their overall growth patterns. These patterns of average increments, however, fail to show the correspondence with microsite distributions that was found with potential (maximum) growth rates.

Yet other features of these trees' growth performance are revealed by scatterplots of each species' diameter increments at all sizes and in all growth years (7 yr for *Simarouba* and the *Cecropia* species; 12 yr for the other six species; Figs. 3 and 4). Substantially differently

shaped increment distributions occur among the nine species. The most striking one is that of *Hymenolobium* (Fig. 3). In this species, there is a broad range of adult tree sizes (39–88 cm diameter) over which all observed diameter increments were substantial (7–18 mm/yr). Above and below this tree size range, however, the increments are well distributed between slightly negative values and *Hymenolobium*'s observed maxima. *Hyeronima* also shows a tendency toward such a window of fast growth (at diameters of ~35–45 cm; Fig. 4), and *Simarouba* has an adult size range (~25–55 cm diameter, Fig. 3) with no negative and few very low increments. All six remaining species, which span all four juvenile microsite groups, show diameter increments that are well distributed between slightly negative values and the species' size-dependent maxima, across all juvenile and adult sizes. The broad spread of annual increments that can be shown by the same individual in successive years is illustrated by the 12 annual increments of the largest measured *Pithecel-*

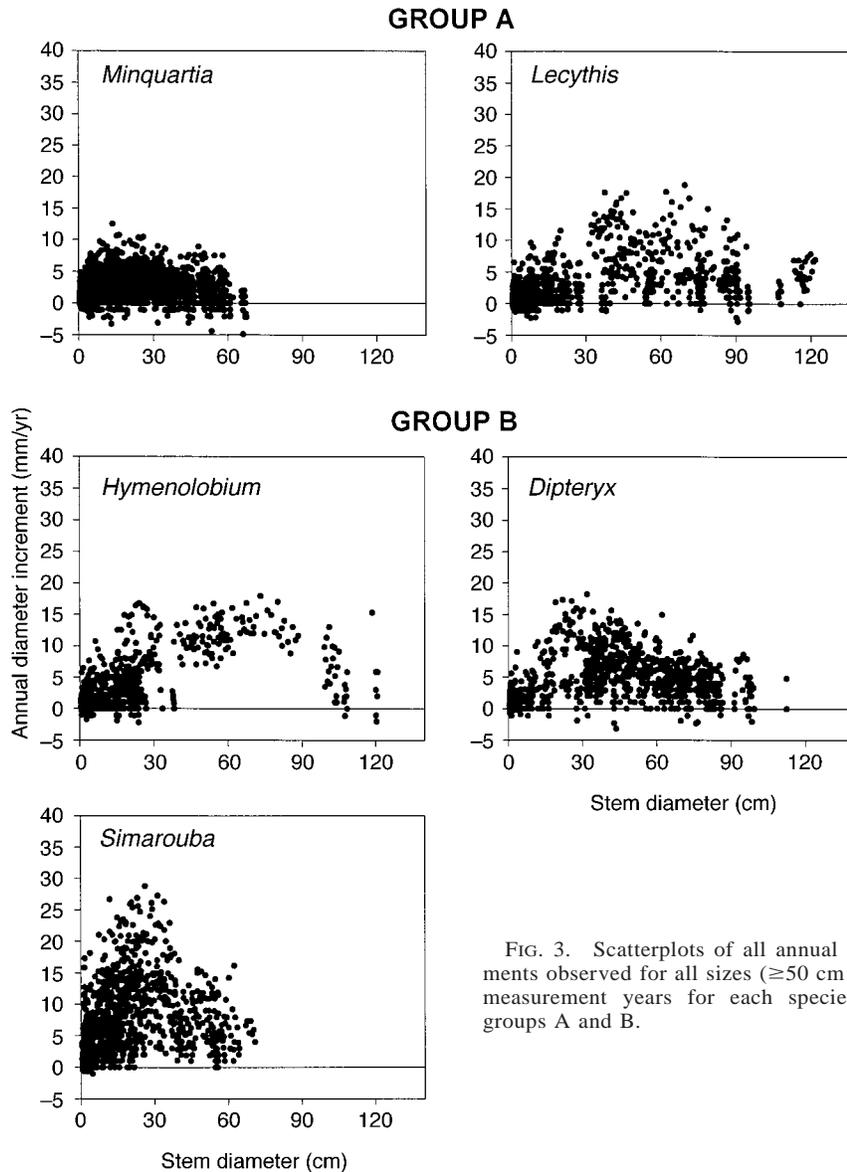


FIG. 3. Scatterplots of all annual diameter increments observed for all sizes ( $\geq 50$  cm tall) and all 12 measurement years for each species of microsite groups A and B.

*lobium* (tree 3073: all the increments at diameters  $> 120$  cm, Fig. 4, *Pithecellobium*).

#### Correlations with diameter and light

An important assumption of forest dynamics models (e.g., SORTIE, Pacala et al. 1994; JABOWA, Botkin 1993) is that tree growth is a geometric function of tree size when environmental constraints are absent. We investigated this relationship for our study species over a broad range of juvenile tree sizes (50 cm tall to 20 cm in diameter). We used partial correlation to separate the effects of tree size (diameter) and available light (see *Methods: Crown illumination*, above) on annual diameter increments (Table 3). Over this size range, annual diameter growth of these species is strongly associated with current crown light environ-

ment. All nine species had significant positive partial correlations, and eight of the nine correlations were at the  $P < 0.01$  level. Growth did not show such a relation with tree size, however. When partial correlations controlled for crown lighting, six of the nine species showed no significant association between diameter and diameter increments, and only two species showed a positive correlation at the  $P < 0.01$  level.

#### Basal-area increments

The capacity of these tree species to add basal area is an aspect of their growth performance that has important implications both for timber production and for assessing these species' potential role in forest-wide carbon budgets. When the five maximum diameter increments in each species/size class (Appendix) are con-

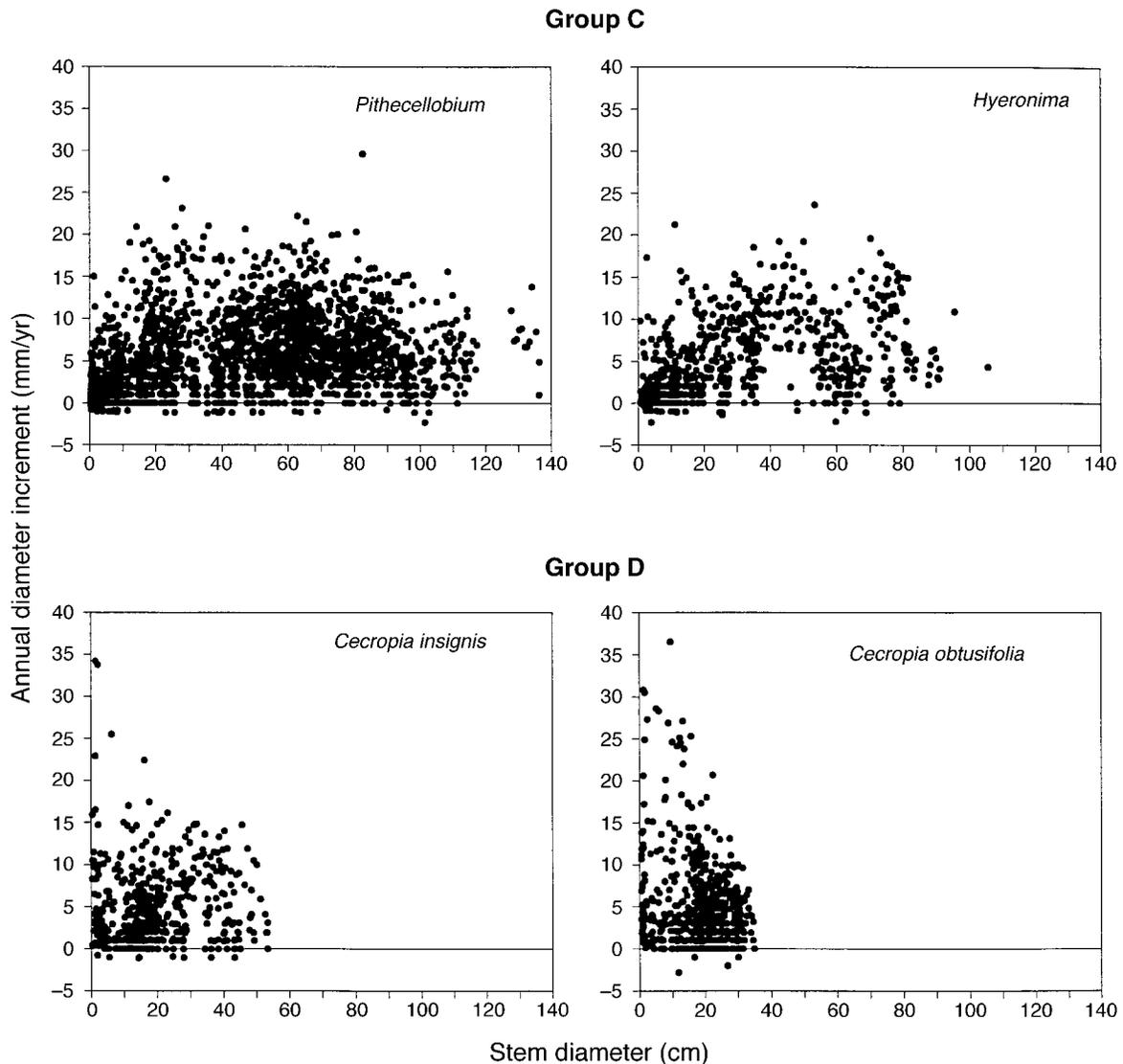


FIG. 4. Scatterplots of all annual diameter increments observed for all sizes ( $\geq 50$  cm tall) and all 12 measurement years for each species of microsite groups C and D.

verted to basal-area increments, striking size-dependent and inter-specific differences are apparent (Fig. 5). First, as expected from the geometric relation of basal area to diameter, the maximum basal-area increments of all nine species greatly increase through ontogeny. For all species except *Cecropia obtusifolia*, potential growth in basal area is substantially (89–380%) greater when the canopy is attained (diameters: 30–50 cm), than when trees are in the lower subcanopy (diameters: 10–20 cm). Second, the basal-area growth of the two pioneers (*Cecropia* spp.) is eclipsed by that of non-pioneer species, beginning with subcanopy tree sizes (diameters: 20–30 cm). Third, by far the largest basal-area increments are exhibited by the emergent trees in their larger diameter classes. As seen in Fig. 5, at 50–70 cm in diameter all five emergent species

show potential basal-area growth that is 2–3 times that of the canopy tree *Miquartia*. The other canopy non-pioneer, *Simarouba*, however, maintains its potential basal-area growth in the range of the emergents. Finally, these patterns do not indicate a general tendency for a levelling off of capacity for basal-area growth in the adult sizes. Most of the non-pioneers showed continued large increases in their maximum basal-area increments after they attained canopy status (diameters:  $>30$  cm).

#### DISCUSSION

This 12-yr study revealed complex intra- and inter-specific patterns of stem growth by canopy trees in an old-growth tropical wet forest. While contradicting several assumptions of current forest-dynamics mod-

TABLE 3. The relations among diameter growth, diameter, and crown light environment for juveniles ( $\geq 50$  cm tall to 20 cm in diameter) of the nine study species in old-growth forest at La Selva, Costa Rica.

Species	Partial correlation of diameter growth		No. of trees
	With crown illumination	With tree diameter	
<i>Minquartia</i>	+0.43***	-0.08	312
<i>Lecythis</i>	+0.18**	+0.16**	194
<i>Hymenolobium</i>	+0.53***	-0.08	81
<i>Dipteryx</i>	+0.37***	+0.35***	156
<i>Simarouba</i>	+0.64***	+0.14*	248
<i>Pithecellobium</i>	+0.51***	+0.08	170
<i>Hyeronima</i>	+0.69***	-0.15	58
<i>Cecropia insignis</i>	+0.29**	-0.37	87
<i>C. obtusifolia</i>	+0.17*	-0.24	111

Notes: For each species, two coefficients are given: (a) for the partial correlation of diameter growth with crown illumination index (see *Methods*), controlling for tree diameter; and (b) for the partial correlation of diameter growth with tree diameter, controlling for crown illumination. Data are from each tree's first census year.

\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ ; one-tailed probabilities (for positive correlations).

els, our findings lend support to the idea that tropical rain forest (TRF) trees can be meaningfully grouped into relatively few functional types in terms of their growth performance. Insights gained from these data

underscore the value of annual measurement of large samples of individuals stratified through ontogeny. Applying this approach to more TRF species, from multiple sites, is likely to greatly extend our ability to model the dynamics of these complex forests.

*Size dependence and ontogenetic switching*

Perhaps most notable was the degree of ontogenetic change in these trees' relative growth performance. No species would be adequately described as "fast" or "slow" growing. In fact, a tree's growth characteristics at one life stage should not be expected to mirror those at other sizes (Oldeman and van Dijk 1991, Grubb 1996). Trees undergo major developmental changes in traits such as root and stem architecture and reproductive allocation. Ontogenetic switching may be common among TRF trees. Examples from our study species are: the lack of correlation between maximum growth rates as small saplings and as young adults; the *Cecropias*' steep ontogenetic decline in inherent growth rates (as found for mean growth of *C. obtusifolia* in a Mexican TRF; Alvarez-Buylla and Martínez-Ramos 1992); and *Lecythis*' dramatically greater growth potential on reaching the canopy. With such marked within-species changes, it is critical to assess growth in all life-history stages when assessing TRF trees for management or forest modeling.

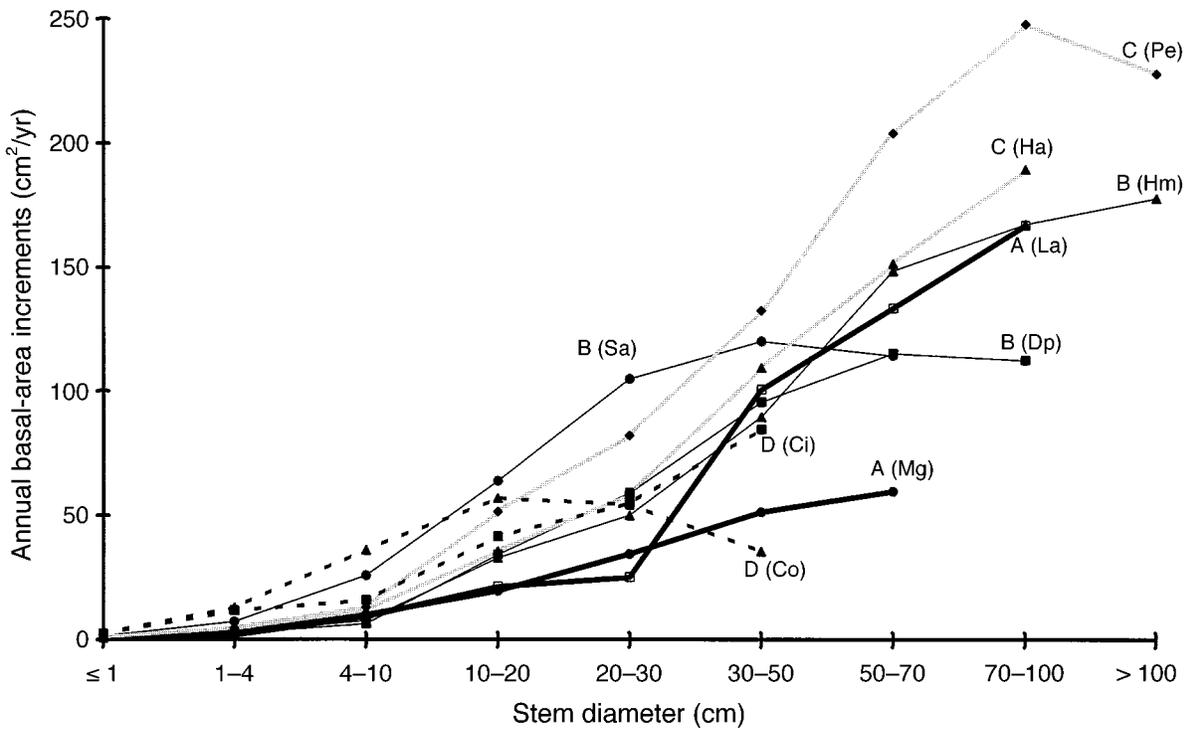


FIG. 5. Basal-area growth potential of the nine tropical rain forest tree species, based on the mean of the five maximum annual basal-area increments in each size class. The five values from each tree species size class are from five different individuals. Sample sizes and statistical comparisons are given in the Appendix. Line labels indicate the microsite group (A–D, Table 2) and species initials (see Fig. 1 for key). Line patterns are keyed to microsite groups: Group A = thick black; Group B = thin black; Group C = grey; Group D = dashed black.

*The multiple dimensions of TRF tree growth*

In recent analyses of interpretation of ecological data, Brown (1995) and Thomson et al. (1996) stressed the value of going beyond the traditional focus on central tendency. Two such approaches in this study led to new insights.

*Maximum growth.*—When data are broadly distributed below an upper bounding relation, the boundary may be ecologically significant (Thomson et al. 1996). When we used the top five increments at each tree size to estimate this “factor-ceiling distribution” (Thomson et al. 1996) for each species’ growth (Fig. 1, Appendix), strong interspecific differences in growth potential were apparent. For eight of the nine species these patterns paralleled the species groupings previously based on juvenile microsites (Clark and Clark 1992). In contrast, average growth rates of juveniles (Fig. 2) did not correspond with the microsite groups. This less clear picture from growth averages is to be expected, given that overall increment distributions are due to complex interactions among size-dependent growth and mortality responses to different microsite conditions, inherent growth capacity at each size, and the particular microsites of sampled individuals. To understand the roles of these variables, their effects need to be separated. The maximum growth rates enabled us to isolate these species’ inherent growth potential from other demographic and environmental factors.

*Overall increment distributions.*—Brown (1995) emphasized the ecological information in the overall shapes and limits of data distributions, particularly when samples are large and well spread over the range of the phenomenon of interest. Our accumulated growth increments, from many years and through ontogeny, provided an opportunity to examine the “growth envelope” for nine species of TRF trees (Figs. 3 and 4). These revealed hitherto unrecognized features of these species. *Hymenolobium* had the most striking pattern (Fig. 3), with adult trees over a very broad size range showing exclusively high growth rates. Once alerted to such “windows of fast growth,” we found on closer inspection that two other species (*Hyeronima*, Fig. 4; *Simarouba*, Fig. 3) also showed size ranges with notably few low or negative increments. Such patterns could be demographically important and should be factored into growth models.

Nevertheless, most species, over most tree sizes, showed a continuum of increments from slightly negative to the observed maxima. In addition to demonstrating the quality and coverage of the data set, these distributions demonstrate broad intraspecific variation in growth rates for all these non-pioneer and pioneer species in old-growth TRF. Such behavior is clearly much better thought of in terms of heterogeneous growth performance within bounds defined by “constraint lines” (Brown 1995: 93), rather than as simple, central-tendency line functions.

*How many functional groups?*

*Ecologically coherent patterns.*—These growth analyses reinforce earlier tentative classification of our study species into four functional groups based on the microsites occupied by their juvenile stages (Table 2). For eight of the nine species, there is a strong and intuitively reasonable correspondence (see *Results: Maximum growth rates*, above) between these microsite groups and the species’ inherent growth potential as juveniles (Fig. 1). This is cause for cautious optimism that the speciose tree communities of TRF actually include relatively few functional types (species groups sharing coherent sets of key ecological traits). There are multiple caveats, however. First, we have not yet assessed these species in terms of either ontogenetic mortality patterns or interactions among growth, mortality, and light levels (cf. Pacala et al. 1993, 1996). So we do not yet know if these or other characteristics conform to the four functional groups. Second, although microsites and patterns of growth potential were correlated for the juvenile stages of these trees, the two Group A species (*Minquartia* and *Lecythis*) had strongly divergent adult growth capacity (perhaps a canopy vs. emergent distinction is an added axis for functional groups?). Third, the growth of one species, *Simarouba*, did not conform to any of the four functional groups when they were defined in terms of both growth capacity and juvenile microsites. Thus, among the nine TRF canopy species that we studied, the evidence suggests five functional types of trees, at least during the juvenile stages. Since we only studied 9 of La Selva’s 339 tree species, we are far from having a sense of the total number of such functional types even in this one forest.

Other researchers have used distinct approaches to try to identify functional groups among TRF trees. Vancly (1991) used pairwise *F* tests to compare growth/size regressions for 237 species in a large set of small inventory plots (0.04–0.5 ha) in Queensland (Australia) forests (trees  $\geq 10$  cm in diameter, measured about every 5 yr). He reduced the large species pool to 41 groups; however, species considered to have “pioneer,” “gap-colonizing,” or “shade-tolerant” characteristics did not sort out consistently among the increment-based groupings. A similar result occurred when Favrichon (1994) combined iterative multivariate analyses and some subjective classification to delineate five functional groups among the 122 more abundant tree taxa in old-growth and logged forest plots in French Guiana. He included in the multivariate analyses each species’ recruitment rates and average growth rates in seven diameter classes, from both managed and unmanaged stands. These five groups corresponded with some other species traits such as seed size and dispersal mode, but there were also numerous cases of apparent mismatches in terms of the trees’ subjectively defined tolerance characteristics. To look for functional groups

among the more abundant 142 tree and shrub species in a Panamanian forest, Condit et al. (1996) similarly used a multivariate analysis of the species' average growth and mortality rates at two sizes, their adult stature (understory or canopy level), and an index of association of small saplings with low-canopy sites. For the canopy trees, most species were clumped at one end and pioneer species were broadly distributed along the rest of this "demographic" axis. Finally, in a plot-based study carried out at La Selva, Lieberman et al. (1985a) used a boot-strapping technique to estimate maximum growth rate (one size-independent growth rate per species) and lifespan from the diameter increments over a 13-yr interval of the 46 more abundant species in the plots (those with 12 or more stems  $\geq 10$  cm in diameter). Combining these estimates with each species' maximum diameter in their 12-ha sample, they defined four species groups.

Although these studies treated several hundred TRF tree species in total, each approached the classification problem in a different way, and their conclusions were subject to important constraints: very limited total sample sizes per species and/or a lack of growth data from all size classes; uncertainty in the increment data due to imprecise measurement in large inventory projects; and usually a lack of temporal replication. It is clearly not yet possible to estimate the nature and number of "functional types" that predominate in these complex tree communities, or even to know if they are comprised of coherent groups of species in terms of key functional traits.

A "super non-pioneer."—The growth performance of *Simarouba* in this study put this species in a category of its own. Although this canopy tree is capable of exceptional diameter growth at La Selva, equivalent to that of the two pioneers, its behavior clearly rules out "pioneer" as an appropriate descriptor. *Simarouba* germinates and establishes in understory conditions (D. A. Clark and D. B. Clark, *personal observation*). We found most of this species' smallest saplings under closed canopy, in low-light microsites (Clark and Clark 1992). As small saplings ( $\leq 4$  cm in diameter), *Simarouba*'s average diameter growth is very slow and indistinguishable from that of the other six non-pioneers (Fig. 2). In terms of maximum growth, however, *Simarouba* diverges remarkably (Fig. 1). Its parabolic curve of growth capacity is strongly reminiscent of that of the two *Cecropia*'s (Fig. 1), but "shifted over" to larger tree sizes. Interestingly, Schulz (1960) presented a similarly shaped growth-diameter curve for this species in Surinam forest, with far greater increments than those of six other canopy species. When Ducrey (1994) tested seedling photosynthetic traits under increasing light levels for seven forest tree species on Guadeloupe, he found *Simarouba amara* to be one of the most plastic, and he characterized it as an "... early successional species, but not really pioneer species. . ." (p. 92). Perhaps other TRF non-pioneer trees will be found to have

this exceptional, parabolic pattern of inherent growth capacity, with peak growth at subcanopy sizes. If more such species are found, an appropriate descriptor will be needed for this pattern. In any case, *Simarouba* cannot be adequately modeled or characterized either as a pioneer or as any of the three non-pioneer functional types we identified among our study species.

#### *Lessons from the real world for TRF forest-dynamics models*

Our findings can be used to assess the applicability to TRF of several features of the tree growth modules in current forest-dynamics models. A common approach in these models (e.g., JABOWA, Botkin 1993; FOREST, Gourlet-Fleury and Montpied 1995) is to characterize species' ontogenetic patterns of inherent growth capacity. Each individual's actual growth is then modeled as the product of this inherent growth potential and growth-reducing factors (environmental constraints such as light limitation or drought). Deriving the inherent growth function for a given tree species, however, is a theoretical and practical challenge, even in the much simpler temperate-zone forests. One type of theoretical growth function (e.g., Botkin 1993) is based on sigmoid growth towards a species' maximum reported size, with parameters adjusted to arbitrarily constrain the timing of the rapid-growth phase. As noted by Pacala et al. (1994), a weakness of this type of formulation is its reliance on statistical outliers (the largest recorded tree sizes). Theoretical inherent growth curves are often assumed to be sigmoid or to show a geometric relation between increment and diameter. An additional assumption in the model SORTIE is that a constant incremental area is added to stems annually, once a threshold adult tree size is reached (the "constant area increment law"; Pacala et al. 1993: 1982).

These assumed relations are used only because empirical data are lacking for these aspects of tree performance. Also an issue is which reference trees to use for assessing a species' inherent (unconstrained) growth potential through ontogeny. As noted by Gourlet-Fleury and Montpied (1995), the relevant maximal growth for forest-dynamics models would not be from open-grown trees, which are architecturally and contextually non-representative of those in forest. These authors, in their work to model the dynamics of old-growth and logged TRF in French Guiana, have estimated forest-level maximum tree growth from size-stratified samples of the five top diameter increments from their study plots (all species combined, logged and old-growth plots combined). In our study, with large samples of increments from many years and through ontogeny, we have extended this approach to the species level. In addition to documenting this way a suite of "inherent growth capacity" functions for TRF canopy species, we can also use our empirical

growth studies to evaluate the applicability to TRF trees of some assumptions of current forest models.

The concept that inherent stem growth potential is a geometric increasing function of tree size (stem radius) at first seems intuitively reasonable; however, as noted by Zeide (1993), such a multiplicative growth relation is not in fact predicted anatomically for trees, given the constant number of cambial cells per stem surface area. Other factors such as crown and root-system allometry could, however, produce such a relation, and recent studies have provided some empirical support for it. Pacala et al. (1994), in their development of the model SORTIE, used extensive empirical data from small forest-grown saplings (0.2–5 cm in diameter) to examine the relations among growth, size, and light for several temperate-forest species. When they analyzed the data using maximum-likelihood techniques, they found that a geometric growth model best fit the data. Similarly, Zeide (1993) tested a number of currently used growth equations against data from Norway spruce plantations, and he found the better-fitting equations to be those based on geometric growth. In our study, however, partial-correlation analysis of diameter increments over a wide range of juvenile sizes (50 cm tall to 20 cm in diameter) contravened the model of geometric growth for most species. Once the strong positive effect of crown illumination had been factored out, the growth rates of six of the nine species were unrelated to tree diameter (Table 3). For two of the nine species, however, growth and diameter were highly significantly correlated. These findings argue for setting aside the geometric-growth assumption and instead basing tree-growth functions in TRF-dynamics models on empirical studies of the dominant species or species groups.

A different assumption of the SORTIE growth module is that of constant area increments (thus declining radial increments) beyond some threshold tree size (Pacala et al. 1993, 1996). Again, as noted by Pacala et al. (1993), this assumption is applied only because of the lack of information on this aspect of growth by their focal species. Our accumulated data on actual growth enable us to test the validity of this assumption for our study species at La Selva. The maximum basal-area increments (Fig. 5) clearly show that these TRF trees lack such an inherent levelling off in basal area addition. For seven of nine species, maximum basal-area increments increased with increasing tree size, usually substantially, well beyond attainment of the canopy (at ~30-cm diameter). Interspecific differences, however, are large (note the wide spread in maximum basal-area increments in any adult size class up to 100 cm in diameter).

Finally, in modeling tree growth it has often been assumed (e.g. Botkin 1993, Parresol et al. 1995) that a species' growth capacity declines to zero as maximum size is approached. For tropical rain forests, where most canopy tree species are locally rare (see Clark and Clark

1996), this aspect of tree growth has not been examined. Our data from this study provided a rare opportunity to assess growth performance at the upper end of tree sizes for TRF canopy trees. For none of our study species do the data (Figs. 1, 3, and 4) indicate a decline to zero growth as trees approach their species' maximum diameter. Even in the species with a strong decline in maximum increments at larger sizes, such as *Simarouba* and *Cecropia obtusifolia* (Fig. 1), many trees at or near maximum size are still growing rapidly (e.g., *Simarouba*, Fig. 3, with numerous increments >5 mm/yr at diameters >50 cm). Thus, the data from this diverse suite of species indicate that modeling growth of larger trees as a function declining to zero at maximum tree size is inappropriate for TRF trees.

The substantial increments observed for the largest trees in our sample raise an interesting question. If the largest individuals we measured are still growing, where is the next larger size class? There in fact could be larger, unsampled trees of these species in the La Selva forest; our samples were not exhaustive. Alternatively, there is no a priori reason to assume these tree populations are in equilibrium. Evidence that the biomass of very large trees is increasing at La Selva (Clark and Clark 1996) suggests that the forest is recovering from past disturbance or is responding to recent atmospheric and/or climatic change. Such a scenario may well apply to many of today's tropical rain forests.

#### *Conclusions and recommendations*

For predicting how tropical rain forests (TRF) will respond to changing conditions, it will almost certainly be necessary to factor these forests' biotic diversity into forest-dynamics models. As Huston (1991) noted, how well a single-species ("big-leaf") approach would work in such models will depend on whether or not the response types represented by the forest's tree species form a continuous gradient. If they do, whole stands might show the smooth adjustment to changes simulated by a single-species (big-leaf) model. If, however, species in a forest show markedly disjunct responses, the peculiarities of given species could greatly affect how the system responds as a whole. Bolker et al. (1995, cited in Pacala and Deutschman 1995) demonstrated a strong impact of biodiversity when they used simulations with the model SORTIE to explore the response of temperate forests to doubled CO<sub>2</sub>. When they modeled a forest composed of nine tree species with empirically based growth and mortality functions, SORTIE predicted a 50–100% greater increase in basal area under elevated CO<sub>2</sub> than was predicted by modeling a single species with parameters averaged from the nine species.

If we are to incorporate species-level or functional-group-level properties into TRF forest dynamics models, we clearly need a better grasp of the range and relative prevalence of growth patterns among the hun-

dreds of tree species coexisting in these forests. We need in-depth assessments of the growth properties of a broad range of TRF tree species, from many site types. Based on the present study, we have several recommendations for the design of such studies.

For a robust assessment of a species' inherent growth capacity, large samples of increments are needed, from many individuals stratified across juvenile and adult sizes. Ideally, growth measurements should be annual. Increments annualized from longer intervals will be lower than the species' maximal rates because of the impacts of interyear climatic variation and forest dynamics on tree growth. For example, the stem growth of adult cohorts of six tree species varied 25–112% among eight consecutive growth years at La Selva (Clark and Clark 1994). Estimates of inherent growth capacity thus necessarily decline with increasing length of census interval. A second advantage of annual measurement is that, in a reasonable amount of time (e.g., a series of 8–12 yr duration), growth can be assessed over a wide range of climatic conditions, including those more favorable for a species. With longer census intervals (e.g., the 5-yr intervals of the 50-ha forest-plot studies; Condit 1995), it will take much longer to obtain temporal replication for estimating a tree species' maximum growth capacity. For example, for the 50-ha plot on Barro Colorado Island in Panama, record ENSO (El Niño/Southern Oscillation) drought conditions have occurred in two of the four 2–5 yr census intervals to date (Condit et al. 1996, R. Condit, *personal communication*).

Assessment of TRF trees' inherent growth capacity will require intensive quality control of the increment measurements and data management (also see Sheil 1995). Measurements should be precise (to  $\pm 0.1$  or 1.0 mm, depending on tree size) and above any buttresses or stem irregularities. Accuracy should be checked by annually remeasuring a set of trees after a several day period has passed, and data should be cross-checked both in the field and through long-term records of the individual trees. Because the data of interest are the highest recorded values, these must be distinguished from measurement or data errors. Without strict quality control, this distinction becomes problematic (cf. Condit et al. 1993a, b, Gourlet-Fleury and Montpied 1995).

Growth analyses should be stratified to treat separately the different life-history stages, through the species' entire size range, rather than developing a single species-wide parameter or growth regression. Measurement data should be treated as absolute increments rather than relative growth rates. The former are much more biologically interpretable. When growth rates are relativized to tree size, they necessarily decline steeply to very low values at larger tree diameters, even when diameter and basal-area increments at these sizes are substantial. Finally, assessing both the maximum growth curve and the shapes of the overall increment distributions through ontogeny is likely to provide im-

portant information about species' growth characteristics that remains hidden when analyses are based on average growth rates.

We know of no other ongoing study of TRF trees that involves annual measurements and adequate species-level samples through all juvenile and adult stages. Because such studies are expensive and difficult to set up and to maintain over the long term, a strategic approach to their design is called for. Only a small subset of species can be studied this way in any forest. Those meriting special attention are the local dominant(s), economically valued species, species representing distinct sectors of the local spectrum of growth/regeneration types, and species under study in other tropical forests. The establishment of such studies would be greatly facilitated by nesting them within the 50-ha forest plots (Condit 1995) that have been set up around the tropics (with all stems  $\geq 1$  cm in diameter already mapped, measured, and identified to species). Landscape-scale studies are also needed, however, because of the limitations of plot-based studies (limited samples for the less abundant species, spatial autocorrelation, and lack of replication by habitat type). Cross-site studies should also be designed to test the variation in TRF tree species' performance under contrasting edaphic and climatic conditions. Progress along these lines will greatly aid current efforts to design rational management for tropical rain forests and to predict their response to global change.

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## APPENDIX

Mean of the top five annual diameter increments in each tropical rain forest tree species size class (constrained to be from five different individuals of each species) during 1983–1995 (1988–1995, for *Simarouba* and the two *Cecropia* species), by stem size class. Different lowercase letters after the means indicate significantly different means in nonparametric pairwise a posteriori tests between species.  $N_{gr}$  = total number of growth increments;  $N_{in}$  = number of individuals from which growth increments were measured.

Species	≤1-cm diameter			>1–4 cm diameter			>4–10 cm diameter			>10–20 cm diameter		
	Mean	$N_{gr}$	$N_{in}$	Mean	$N_{gr}$	$N_{in}$	Mean	$N_{gr}$	$N_{in}$	Mean	$N_{gr}$	$N_{in}$
<i>Minquartia</i>	4.0abc	463	122	5.2abc	877	110	8.2abc	943	103	9.3a	633	66
<i>Lecythis</i>	4.0ab	349	76	4.5a	764	89	7.5ab	428	54	8.1a	267	32
<i>Hymenolobium</i>	3.1a	50	20	5.4ab	247	33	6.7ab	211	28	11.7abc	203	27
<i>Dipteryx</i>	3.6a	570	134	5.4ab	252	38	4.8a	109	13	11.9ab	62	8
<i>Simarouba</i>	6.8abc	238	87	15.3abc	446	93	17.2bc	249	65	23.9bc	301	65
<i>Pithecellobium</i>	5.5abc	239	68	10.1abc	291	55	11.1abc	348	46	17.4abc	225	41
<i>Hyeronima</i>	...	...	...	8.8abc	105	17	9.0abc	195	26	15.0abc	206	27
<i>Cecropia insignis</i>	11.6bc	14	13	24.4bc	44	26	13.0abc	80	20	16.8abc	231	44
<i>C. obtusifolia</i>	11.9c	18	17	26.8c	38	26	26.2c	62	25	25.2c	250	64
$P_{\dagger}$	0.0001			0.0000			0.0000			0.0000		

## APPENDIX. Extended.

Species	>20–<30 cm diameter			30–50 cm diameter			>50–70 cm diameter			>70–100 cm diameter		
	Mean	$N_{gr}$	$N_{in}$	Mean	$N_{gr}$	$N_{in}$	Mean	$N_{gr}$	$N_{in}$	Mean	$N_{gr}$	$N_{in}$
<i>Minquartia</i>	8.6a	455	68	8.5ab	608	78	7.1a	252	31	...	...	...
<i>Lecythis</i>	6.5a	97	11	15.4abc	106	11	13.7ab	102	13	12.8ab	146	17
<i>Hymenolobium</i>	12.2ab	166	20	13.6abc	48	10	15.6ab	49	7	12.8ab	23	5
<i>Dipteryx</i>	15.3ab	55	9	15.5abc	253	28	12.7ab	193	23	9.0a	205	24
<i>Simarouba</i>	26.6b	138	41	22.6c	160	32	13.0ab	99	18	...	...	...
<i>Pithecellobium</i>	19.8b	191	33	19.3c	373	50	20.0b	526	67	19.7b	447	59
<i>Hyeronima</i>	13.2ab	89	15	16.9bc	138	19	16.9b	134	19	16.1ab	74	9
<i>Cecropia insignis</i>	13.2ab	104	21	14.4abc	92	19	...	...	...	...	...	...
<i>C. obtusifolia</i>	14.7ab	218	51	7.0a	41	10	...	...	...	...	...	...
$P_{\dagger}$	0.0000			0.0000			0.0009			0.006		

## APPENDIX. Extended.

Species	>100-cm diameter		
	Mean	$N_{gr}$	$N_{in}$
<i>Minquartia</i>	...	...	...
<i>Lecythis</i>	...	...	...
<i>Hymenolobium</i>	9.8	35	5
<i>Dipteryx</i>	...	...	...
<i>Simarouba</i>	...	...	...
<i>Pithecellobium</i>	12.6	90	11
<i>Hyeronima</i>	...	...	...
<i>Cecropia insignis</i>	...	...	...
<i>C. obtusifolia</i>	...	...	...
$P_{\dagger}$	...		

† Probabilities are from Kruskal Wallis tests within size classes.