GETTING TO THE CANOPY: TREE HEIGHT GROWTH IN A NEOTROPICAL RAIN FOREST

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Abstract. There is still limited understanding of the processes underlying forest dynamics in the world's tropical rain forests, ecosystems of disproportionate importance in terms of global biogeochemistry and biodiversity. Particularly poorly documented are the nature and time scale of upward height growth during regeneration by the tree species in these communities. In this study, we assessed long-term height growth through ontogeny for a diverse group of canopy and emergent tree species in a lowland neotropical rain forest (the La Selva Biological Station, northeastern Costa Rica). Species were evaluated based on annual height measurements of large samples of individuals in all postseedling size classes, over a 16-yr period (>11 000 increments). The study species were seven nonpioneers (*Minquartia guianensis, Lecythis ampla, Hymenolobium mesoamericanum, Simarouba amara, Dipteryx panamensis, Balizia elegans,* and *Hyeronima alchorneoides*) and two pioneers (*Cecropia obtusifolia* and *Cecropia insignis*). For each species, inherent height growth capacity was estimated as the mean of the five largest annual height increments (from different individuals) in each juvenile size class (from 50 cm tall to 20 cm in diameter). All species showed marked ontogenetic increases in this measure of height growth potential. At all sizes, there were highly significant differences among species in height growth potential. The two *Cecropia* species consistently showed the highest observed maximum height increments as smaller juveniles (≤4 cm in diameter). Among the nonpioneers, *Simarouba* had the highest growth potential across all juvenile sizes. For all species, mean annual height increments in all juvenile size classes were very much lower than the species' potential growth rates and reflected the impacts of frequent periods of zero growth and major height losses from physical damage. Because of the same factors, maximum net height increments declined over increasing measurement intervals (1–15-yr periods). With only one exception (*Simarouba amara* saplings ≤1 cm in diameter that survived 10 yr), the annual height growth increments of these species showed no significant temporal autocorrelation. For the seven nonpioneer species, we estimated the minimum time required to grow from 50 cm tall saplings to 10 cm diameter trees, based on their greatest net height increments over increasing intervals. Estimated passage times increased from 7–33 yr, when based on maximum 5-yr height increments, to 37–83 yr, when based on maximum net height growth over 15 yr for the six longest studied (nonpioneer) species. Given the erratic height growth trajectories found for these juvenile trees in this 16-yr study, it is clear that much longer term observation is required. Still unknown are the actual growth trajectories that characterize successful regeneration in each of our focal species, how much time successful trees spend as suppressed juveniles, and the number of times they experience and recover from major physical damage.

Key words: Costa Rica; inherent growth capacity; La Selva; ontogenetic switching; physical damage; pioneers; tree height growth; tree regeneration; tropical rain forest; suppression, growth of juvenile trees.

Introduction

There is a pressing need for better process-level understanding of the dynamics of tree communities in the moist and wet tropics. In addition to the great biodiversity that they harbor (cf. Gentry 1992), tropical evergreen forests are disproportionately important in the world carbon budget. Only 14% of potential global vegetation by area (Melillo et al. 1993), they are estimated to account for 32% (Field et al. 1998) to 36% (Melillo et al. 1993) of potential global net primary production on land. Further, recent modeling and empirical studies of these forests (e.g., Clark and Clark 1994, Kindermann et al. 1996, Tian et al. 1998), suggest that they are highly responsive to climatic variation and thus could significantly shift their net carbon balance with on-going global climate change. Realistic forest dynamics models of these ecosystems will be needed for simulation of how these complex communities function and how they will respond to future environmental change. Empirical as-

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sessments of the growth patterns of representative tree species in these forests will be fundamental for the development of such models.

The extremely high species diversity of tree communities in the moist tropics (cf. Foster and Hubbell 1990, Valencia et al. 1994) is accompanied by local rarity of most of the tree species (cf. Hubbell and Foster 1986, Kochummen et al. 1990, Lieberman and Lieberman 1994, Clark et al. 1999). Thus, demographic analyses at the species level have concentrated on the trees that are relatively common in a given forest. For those species that have been studied, data on growth patterns have been based on multiple-year intervals (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). Such supra-annual censuses impede the assessment of species' maximum growth potential, because variations in climatic conditions and forest dynamics are likely to produce substantial within-interval variation in growth performance. Growth studies to date have focused on stem diameter increments, and the process of height growth to the canopy by tropical trees remains poorly understood.

Since 1983, we have been carrying out long-term demographic studies of an ecologically diverse suite of canopy tree species in a lowland neotropical forest. Annually, we have measured diameter growth, height growth (to 16–17 m), physical damage, survival, and microsite characteristics for large samples of individuals from all postseedling juvenile size classes of nine species that range from pioneers (*Cecropia* spp.; cf. Swaine and Whitmore 1988) to long-lived emergents. The long-term records from this study provide an exceptional opportunity to characterize the potential and realized growth characteristics of these species through regeneration. A comparative analysis of the diameter growth of these species (Clark and Clark 1999) revealed major ontogenetic shifts in relative performance, underlined the marked differences between average and potential growth through a species' life history, and provided evidence of coherent functional groups among the nine species.

In this paper, we build on this work by analyzing a heretofore neglected aspect of tropical tree demographic performance: height growth during regeneration. In a very real sense, height growth is what directly determines how or if a juvenile tree is going to make it to the canopy. The process of growing up toward the canopy, however, has not been documented for tropical trees. How do potential and realized height growth vary among the canopy tree species in tropical rain forest? Are there ontogenetic changes in their relative height growth performance? How consistent through time is the growth of juvenile trees of these species? Are some individuals consistently fast growers that are much more likely to reach the canopy? Are the majority, in contrast, consistently growing slowly through time?

The data analyzed in this paper consist of annual height increments of nine species of canopy and emergent trees, for all post-establishment stages up to sub-canopy juveniles. Although most of these species are locally rare, we obtained samples of individuals from all juvenile size classes by extensive searches over ~250 ha of old-growth forest. The more than 11 000 height increments come from individuals censused annually for up to 10–15 yr.

We use these data to address the following questions. (1) What is each species' inherent capacity for height growth in old-growth conditions? (2) What is the relationship between this growth potential, based on maximum observed increments, and average rates of height growth? (3) How does height growth vary ontogenetically in these species? (4) Are an individual's height growth increments temporally autocorrelated? (5) What do these patterns imply about the time required for these species to grow to the canopy? Although our study is in one site, the focal species cover a broad spectrum of tropical tree life history types. We conclude the paper by discussing the aspects of our findings from La Selva that are likely to be representative of tree regeneration processes over a wide range of tropical moist forests.

METHODS

Study site and species

The 1550-ha La Selva Biological Station of the Organization for Tropical Studies (OTS) is in the Atlantic 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 includes 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% per year for trees ≥10 cm 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 nine study species (Table 1). One focus was emergents, trees with mature crowns extending above the average canopy level. Because emergents experience an extreme microhabitat range through ontogeny, it has been hypothesized that they share ecological and physiological characteristics (Mooney et al. 1980, Bazzaz 1984) and, thus, may constitute a well-defined tree "functional group." Because of their large stature, emergents can also greatly affect

TABLE 1. The nine tree species under long-term study at La Selva, Costa Rica.

Microsite group†	Species and family	Voucher specimen	Stratum attained	Maximum diameter, cm (N)‡	Maximum measured ht., m (N)§
A	*Minquartia guianensis* Aubl. Olacaceae	G. Herrera 2250	canopy	82 (115)	⋯
A	*Lecythis ampla* Miers Lecythidaceae	R. Robles 2208	emergent	161 (67)	51 (2)
B	*Hymenolobium mesoamericanum* H. C. Lima Papilionoideae	R. Aguilar 19	emergent	156 (34)	58 (5)
B	*Dipteryx panamensis* (Pittier) Record & Mell Papilionoideae	R. Robles 1199	emergent	187 (140)	54 (30)
B	*Simarouba amara* Aubl. Simaroubaceae	R. Robles 1670	canopy	81 (47)	⋯
C	*Balizia elegans* (Ducke) Barneby & J. W. Grimes‖ Mimosoideae	B. Hammel 17319	emergent	137 (198)	55 (6)
C	*Hyeronima alchorneoides* Allemao Euphorbiaceae	Chacon 751	emergent	187 (98)	50 (17)
D	*Cecropia insignis* Liebm. Cecropiaceae	W. Burger 11135	canopy	54 (21)	⋯
D	*Cecropia obtusifolia* Bertol. Cecropiaceae	R. Robles 1446	canopy/subcanopy	35 (10)	⋯

Notes: Vouchers are in the Herbario Nacional de Costa Rica (except the *Hyeronima* voucher, which is at the Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica). Ellipses indicate that data are not available.

† Microsite groups from Clark and Clark (1992): A, species associated with dark, non-gap microsites through regeneration; B, species that establish in dark, non-gap sites but, with increasing sapling size, increase in crown illumination and are increasingly biased toward gap/building microsites; C, species that are strongly associated with gaps as small saplings and again as subcanopy trees but survive well as intermediate-sized juveniles as the canopy closes; D, species associated with gaps and/or higher crown illumination through all juvenile stages.

‡ Maximum bole diameter (above buttresses) is from all adult trees in the study; *N* is the number of measured trees.

§ Maximum measured heights for the five emergent species (D. B. Clark, *unpublished data*) are from adult trees measured at La Selva with the laser altimeter (see *Methods*); *N* is the number of measured trees.

‖ Formerly *Pithecellobium elegans* Ducke.

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 because of their typically low densities (Foggie 1960, Knight 1975, Clark and Clark 1987, 1996). Secondly, in an attempt to sample over the entire 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 contrasting patterns of microsite occupancy through regeneration for these nine species (Table 1). Thirdly, we focused on timber trees of economic value (all but the two *Cecropia* spp.). In this paper, we will refer to all species but the two *Cecropia* species by genus.

Six species (*Minquartia, Lecythis, Hymenolobium, Dipteryx, Balizia,* 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: *Simarouba,* a nonpioneer (Clark and Clark 1999), and two pioneer species (Swaine and Whitmore 1988), *Cecropia insignis* and *C. obtusifolia.* 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* species, trees are reproductive at diameters <30 cm).

Species samples and annual censuses

As in other tropical moist or wet forests, most trees and lianas are rare at La Selva (83% of 269 species in three 4-ha inventory plots had densities ≤1 tree/ha at diameters ≥10 cm; Lieberman et al. 1985*a, b*). For many species, certain juvenile size classes are also scarce (e.g., 10–30 cm diameter *Dipteryx,* 0.25 trees/ha; Clark and Clark 1987). For many tropical trees, therefore, analysis of performance in all life history stages cannot be based on forest inventory plots, although the 50-ha plots distributed around the tropics (Condit 1995) greatly extend the number of species that can be studied this way in plots.

To assess performance of our nine focal species in all size classes and microhabitats, we used landscape-scale sampling. The sampling methods (detailed in Clark and Clark 2000) were designed to accumulate individuals from all post-establishment size classes (≥50 cm tall), in samples that were unbiased in terms of microsite and tree condition, and that were distrib-

uted over a large forest area (~250 ha of old growth, excluding swamps), thus providing replication across environmental gradients. For five species (*Lecythis, Hyeronima, Hymenolobium,* and the two *Cecropia* species), we also added annually to the species samples any newly encountered seedlings (plants <50 cm tall); for two other species, seedlings were added in early years of the study (*Minquartia,* 1983; *Balizia,* 1983, 1985). All sampled individuals were marked and mapped and have been censused annually until confirmed to be dead in successive censuses. They are measured in the same sequence during January–June, to maintain approximately annual intercensus intervals and thereby control for any seasonal effects on growth (e.g., in 1994/1995, the remeasurement interval for 94% of the trees ($N = 2011$) was 365 ± 16 d). Data analyzed in this paper are from the period 1983–1999.

Annual height measurements

Height was measured vertically from the upslope side of the base of each tree's main stem. Measurements with all techniques were to the nearest centimeter. Height of saplings ≤1.5 m tall was measured as the vertical distance between the stem base and the base of the highest live meristem, for all species but *Lecythis.* For the shrub-like saplings of *Lecythis,* and for all individuals >1.5 m tall of all species, height was to the highest live leaf (or highest live twig, if the tree was deciduous). To measure height, we used a folding wooden ruler for plants <2 m tall, and a 15-m expandable measuring pole (Hastings Fiber Glass Products, Hastings, Michigan, USA) for all individuals up to ~16 m tall (one person raising the pole, a second acting as "spotter" to assess when the pole reached the level of the top of the tree crown) and for occasional taller trees that could also be measured this way because of special circumstances (e.g., adjacent fallen logs to stand on). In 1999, we used a precision laser altimeter (Impulse 200LR, Laser Technology, Engelwood, Colorado) to measure heights of 42 trees taller than 16 m, to obtain 5-, 10-, or 15-yr increments for trees that had grown beyond the reach of the measuring pole. To test for repeatability of the data with this method, we remeasured 17 trees (height range: 1483–2676 cm) after 1 d. The maximum difference was 5% for 15 of the 17 trees; for two trees, repeat measurements differed by 8–9% (absolute height differences were 152 and 170 cm).

When annual height growth was positive, the increment was calculated as the difference between successive annual height measurements, divided by the quantity [number of days between measurements/365]. In cases of net height loss, annual height increment was calculated as the difference between heights in the two years.

Data quality control was an ongoing priority. Only three experienced field technicians and the authors measured the trees. When each height measurement was taken, it was checked against the previous year's height (on the field data forms). In cases of large decreases or increases, the tree was remeasured and supporting observations (apparent cause of height loss, remeasurement to confirm substantial growth) were noted on the field sheets. Before each year's census, we performed a measurement quality check based on remeasurement of a set of trees after an interval of two to several days. In a representative check, for 23 trees spanning the range of sizes measured with the ruler or expandable pole, repeat height measurements showed a mean difference of 2.0% (Clark and Clark 1992). Data quality was further assessed by checking the master database for consistency of a tree's measurements across years. In the few cases of clear contradictory data (e.g., a large height loss or gain bracketed by years with nearly constant height), supporting information was sought on the field data sheets; any inconsistent data were corrected, when this could be done unambiguously, or were eliminated (flagged as "no data").

Stem diameter measurements

For individuals <4 cm in diameter, maximum stem diameter was measured with calipers to the nearest 0.1 mm at a marked point of measurement (POM) below the lowest branch and away from stem irregularities. We measured 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 was moved upward. Boles ≥4 cm in diameter were measured with a diameter tape to the nearest millimeter, rounding down. The tape was passed under any vines or roots on the stem. Boles were measured at 130 cm above the ground ("breast height") when this point was not affected by buttresses or major stem deformities; otherwise, the POM was above such irregularities, often 5–7 m above the ground. Each tree's POM was marked by an aluminum nail 10 cm higher on the bole. Further details on diameter measurements are given in Clark and Clark (1999).

Stem damage

In each annual census, each tree was evaluated for major physical damage, leader dieback, and resprouting (see Clark and Clark 1991). Supporting observations (overlying debris, new gaps, insect damage) were also noted on the field data sheets.

RESULTS

Maximum height growth through ontogeny

Height growth potential varied substantially intra- and interspecifically among these rain forest tree species. Growth potential at each size (Table 2) was estimated as the mean of the five largest 1-yr height increments observed during the 16-yr study period (constrained to be from five different individuals per

TABLE 2. Height growth potential of nine tree species, by size class, in old-growth forest of La Selva, Costa Rica.

| | <50 cm tall | | | | ≥50 cm tall, ≤1 cm diameter | | | |
| | Height increment (cm/yr) | | Sample size† | | Height increment (cm/yr) | | Sample size† | |
Species	Mean‡	Max.	N_{gr}	N_{in}	Mean‡	Max.	N_{gr}	N_{in}
Minquartia	51[a]	68	143	47	76[cde]	100	714	142
Lecythis	38[a]	50	87	47	76[bcde]	115	442	91
Hymenolobium	21[a]	29	58	31	74[abcde]	152	78	29
Dipteryx	33[a]	50	23	16	73[bcde]	112	651	143
Hyeronima	. . .	65	3	2	. . .	167	16	5
Balizia	33[a]	66	138	38	120[abcde]	185	283	79
Simarouba	22[a]	59	10	7	132[abce]	171	331	122
Cecropia insignis	. . .	178	1	1	150[abe]	186	16	15
C. obtusifolia	. . .	173	3	3	126[abcde]	255	18	17

Notes: Data are the mean and maximum of the top five annual height increments during 1983–1999 (1988–1999 for *Simarouba* and *Cecropia* spp.). Means are shown for classes with $N \geq 7$ trees. Ellipses indicate inadequate sample size. Results of Kruskal-Wallis tests of the top five height increments (from five different trees per species) are reported for all nine species (P_9) and excluding the two *Cecropia* species (P_{-C}), by size class: <50 cm tall, $P_9 = 0.02$, $P_{-C} = 0.10$; ≥50 cm tall, $P_9 = 0.01$, $P_{-C} = 0.04$; 1–4 cm diameter, $P_9 = 0.000$, $P_{-C} = 0.004$; 4–10 cm diameter, $P_9 = 0.000$, $P_{-C} = 0.013$; 10–20 cm diameter, $P_9 = 0.004$, $P_{-C} = 0.006$.

† N_{gr}, no. growth increments measured; N_{in}, no. individuals measured.

‡ Different superscript letters indicate significant differences between species ($P \leq 0.01$) using the Mann-Whitney U, a posteriori pairwise comparison.

species, to permit statistical comparisons among species).

All species showed a marked ontogenetic increase in height growth potential, with the biggest increases occurring at the smaller sizes (Table 2). Patterns varied among the species, however. The ontogeny of height growth potential in the two *Cecropia* species clearly distinguished them from the seven nonpioneers. They were the only two species with annual height increments >1 m as seedlings (<50 cm tall); however, on reaching the largest juvenile size class (diameters 10–20 cm), both *Cecropia* species showed decreased height growth potential compared to that at 1–10 cm diameter. In contrast, most of the seven nonpioneer species showed consistent, marked increases in maximum height growth between all successive pairs of juvenile size classes (the two exceptions were *Lecythis*, whose height growth potential declined at diameters of 10–20 cm, and *Balizia*, with a similar decline on reaching 4–10 cm diameter). *Balizia* and *Simarouba* showed especially notable increases in height growth potential between the two smallest size classes.

At all juvenile sizes ≥50 cm tall, there was significant interspecific variation within the entire species group (Table 2). Although the values for height growth potential suggest functionally different groups among the nonpioneers in all but the smallest juveniles, pairwise species comparisons failed to show clear-cut groups within most size classes (Table 2). Thus, these species appear to have largely similar capacities for height growth during regeneration. The exception is *Simarouba,* which consistently showed the greatest height growth potential among the nonpioneers at all sizes ≥50 cm tall. In both of the two largest juvenile size classes, *Simarouba* had the greatest mean maximum growth increments of all species, including the two *Cecropia* species.

The maximum observed annual height increments at each size (Table 2) showed that all of these species can grow 1 m in height in a year at all juvenile sizes above 50 cm tall. Further, all species were capable of growing 2–3 m in height in a year in at least some juvenile stages. Two species, *Simarouba* and *Cecropia insignis*, had height increments of 4 m/yr as juveniles 4–20 cm in diameter.

Mean height growth through ontogeny

Compared to maximum growth rates, average annual height increments (Fig. 1) gave a very different picture of the performance of these trees through ontogeny. For saplings up to 4 cm in diameter, mean 1-yr height increments of the nonpioneers were nearly all <20 cm. The extreme case is that of *Hyeronima* at 1–4 cm diameter, with a negative mean annual height increment. These means, however, were consistently associated with very large standard deviations across species and size classes (data not shown).

As for the maximum height increments, mean annual height growth rates (Fig. 1) showed highly significant differences among species, in all juvenile size classes ($P < 0.001$, Kruskal Wallis comparisons of species within size classes). At diameters up to 10 cm, the two *Cecropia* species had the greatest average height increments (with the notable exception of *C. obtusifolia* at 1–4 cm diameter). As with maximum growth rates, *Simarouba*'s mean increments tended to be higher than those of most other nonpioneer species. Four of the nonpioneers showed substantially increased mean height increments at diameters of 10 to 20 cm.

TABLE 2. Extended.

1–4 cm diameter				4–10 cm diameter				10–20 cm diameter			
Height increment (cm/yr)		Sample size†		Height increment (cm/yr)		Sample size†		Height increment (cm/yr)		Sample size†	
Mean‡	Max.	N_{gr}	N_{in}	Mean‡	Max.	N_{gr}	N_{in}	Mean‡	Max.	N_{gr}	N_{in}
122[cde]	128	1082	121	179[bcde]	208	1128	100	204[abcd]	311	320	43
141[bcde]	181	993	92	178[bcde]	246	541	57	142[bde]	151	177	27
148[abcde]	226	317	36	158[cde]	174	251	29	257[abcd]	390	108	15
153[abcde]	246	365	46	188[bcde]	225	128	14	—	187	13	2
124[bcde]	156	126	20	192[bcde]	256	223	25	242[abcd]	371	103	17
220[abc]	262	398	56	170[cde]	177	446	43	215[abcd]	264	82	21
226[abc]	242	580	103	321[ab]	433	384	77	302[abc]	411	105	35
297[abc]	402	65	32	267[abce]	430	90	21	185[abcde]	263	36	10
207[abcd]	328	45	30	317[ab]	356	60	22	168[bcde]	203	11	7

Temporal autocorrelation in height growth

When analyzed in two ways, our data showed little or no temporal autocorrelation in the annual height increments of juveniles of these species. We assessed the correlation (Pearson's r) between a tree's height increment in one year and its increment in the following year for all successive pairs of annual height growth measurements in our long-term records (in the 38 species/size classes with >10 increment pairs). No species/size class showed a correlation ≥0.50 between pairs of successive height increments, and, in most cases (28 of 38), the correlation was ≤0.20. Because multiple pairs of increments in a data set could be from a single individual, the data are not strictly independent and correlations are likely to be biased upward (we therefore did not calculate significance levels). In a
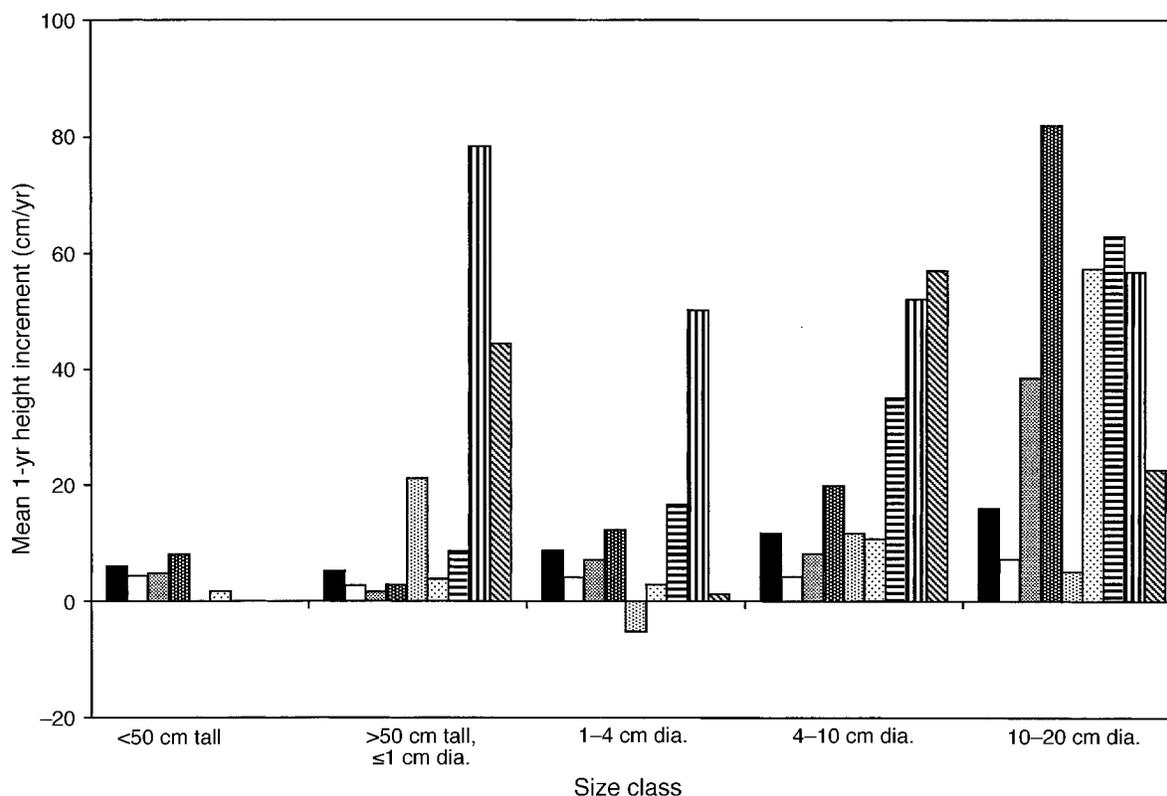

FIG. 1. Mean annual height increments of the nine study species in all juvenile size classes (by height and/or diameter, dia.) in old-growth forest at La Selva, Costa Rica (sample sizes are given in Table 2). For each size class, species are (from left to right): *Minquartia, Lecythis, Hymenolobium, Dipteryx, Hyeronima, Balizia, Simarouba, Cecropia insignis,* and *C. obtusifolia.* Means are given for classes with measurements of >10 height increments and at least six trees and are based on all annual height increments in each species/size class during 1983–1999 (1988–1999 for *Simarouba* and the *Cecropia* species).

second analysis, we assessed the correlation (Pearson's *r*) between a tree's height growth in the first year and its growth in each of the nine subsequent years for those species with ≥10 trees with a complete 10-yr series of successive height increments. For saplings ≥50 cm tall and ≤1 cm in diameter, we had sufficient samples for five of the nine species. *Minquartia, Lecythis,* and *Dipteryx* showed low correlations (0.09–0.39) even between the first pair of years, and very low correlations (<0.15 to negative) between the initial increment and increments in most later years in the series. For *Balizia*, the initial height increment was more strongly related to those of years 2 and 3 ($r = 0.65$ in both cases; $N = 12$ trees), but the correlations then dropped substantially (five of the eight correlations with subsequent years were <0.20 to negative). In contrast, *Simarouba* at these small sapling sizes showed relatively high correlations between the initial annual height increment and those in nearly all of the following nine years (correlations with years 2–10, respectively: 0.92, 0.81, 0.48, 0.79, 0.53, 0.65, 0.76, 0.88, 0.74; $N = 14$ trees). In the next larger juvenile size class (>1–4 cm in diameter), however, none of the six species for which we had adequate samples of trees with 10-yr series (*Minquartia, Lecythis, Hymenolobium, Dipteryx, Balizia,* and *Simarouba*) showed strong correlations between initial height increments and those in years 2–10. Nearly all correlations were either negative or <0.30, and the highest was 0.52. In the >4–10 cm diameter class, *Minquartia, Lecythis, Hymenolobium, Hyeronima,* and *Balizia* all showed a similar lack of association between initial and subsequent increments. *Simarouba* had relatively high correlations between the initial increment and those of years 2–4 (0.70, 0.55, and 0.916, respectively; $N = 10$ trees), but correlations with subsequent increments were very low (0.19 to −0.64).

Interrupted progress to the canopy

The large differences between mean and maximum height increments for juveniles of these species, and the lack of temporal autocorrelation in height growth records of juveniles both reflect the high frequency of cases in which suppression and physical damage impede tree growth toward the canopy in the La Selva forest. In all juvenile size classes, substantial percentages of annual height increments were zero to negative for these canopy trees (Fig. 2). Averaged across species and in all size classes, a mean of 22–29% of annual increments were negative or zero.

Do such growth failures occur during cases of successful regeneration by these canopy tree species, or are they restricted to the individuals that fall by the wayside? For the seven nonpioneer study species, the long-term records show that such setbacks are normal experiences for juvenile trees that survive long periods in this forest. We analyzed the growth records of juvenile trees for which we had a complete 10-yr series of successive annual height increments (Table 3).

Across the size range from saplings 50 cm tall to trees 10 cm in diameter, these nonpioneer species averaged 86–94% of individuals with at least one year of no net height growth in a 10-yr series (we lack adequate samples of 10-yr series of height increments for the pioneers, the two *Cecropia* species). Substantial negative height increments were also common. For the smallest saplings (≤1 cm diameter), an average of 29% of individuals, across species, had at least one annual height loss of ≥50 cm. In the three larger juvenile size classes, an average of 34–36% of individuals showed losses of 1 m or more in height in at least one of the 10 years. In all size classes, trees showed maximum 1-yr height losses of 2–13 m.

Case studies of individuals that experienced physical damage or long suppressed periods are shown in Fig. 3a–c. These 15–16 yr histories illustrate three features of nonpioneer tree regeneration at La Selva: (1) juveniles can survive long periods with no appreciable height growth; (2) incidents of physical damage from falling branches or trees can produce major height losses in juvenile trees; and (3) saplings of these species can survive and gradually recover from such height losses, although recovery can take many years. For comparison, Fig. 3d shows the growth history of the juvenile tree with the greatest long-term height gain in our study (a *Simarouba* that grew 110 cm/yr over 11 yr). This tree, which showed substantial growth in all 11 yr and which escaped major physical damage during this entire period, is, however, highly exceptional. For the only other tree with similarly high long-term height increments (*Balizia* #3075, which averaged 106 cm height growth/yr over 10 yr), three successive height increments during the 10 yr were negative.

Passage times to reach the lower subcanopy

We combined our data on height growth rates and diameter/height allometry to estimate the minimum time that these species require to grow from the smallest saplings (50 cm tall and ≤1 cm in diameter) to trees 10 cm in diameter, the minimum size cutoff for many long-term forest plot studies. We did not extend this analysis to the 10–20 cm diameter class, because of the increased potential for underestimating maximum growth rates of trees this size when the study individuals grow past our top measurement height. For each diameter size class, we used the maximum observed height for each species (Table 4) to calculate the height range (in centimeters) corresponding to each diameter size class. We then calculated passage times by dividing each species' height range in a size class by the maximum height increment observed for trees in that size class over 5-, 10-, and 15-yr intervals (Table 5a–c). Three limitations in the data need to be taken into account in interpreting these data: (1) sample sizes are low for the two *Cecropia* species; (2) in most cases, sample sizes decline with increasing intervals; and (3) in the largest juvenile class, some individuals went
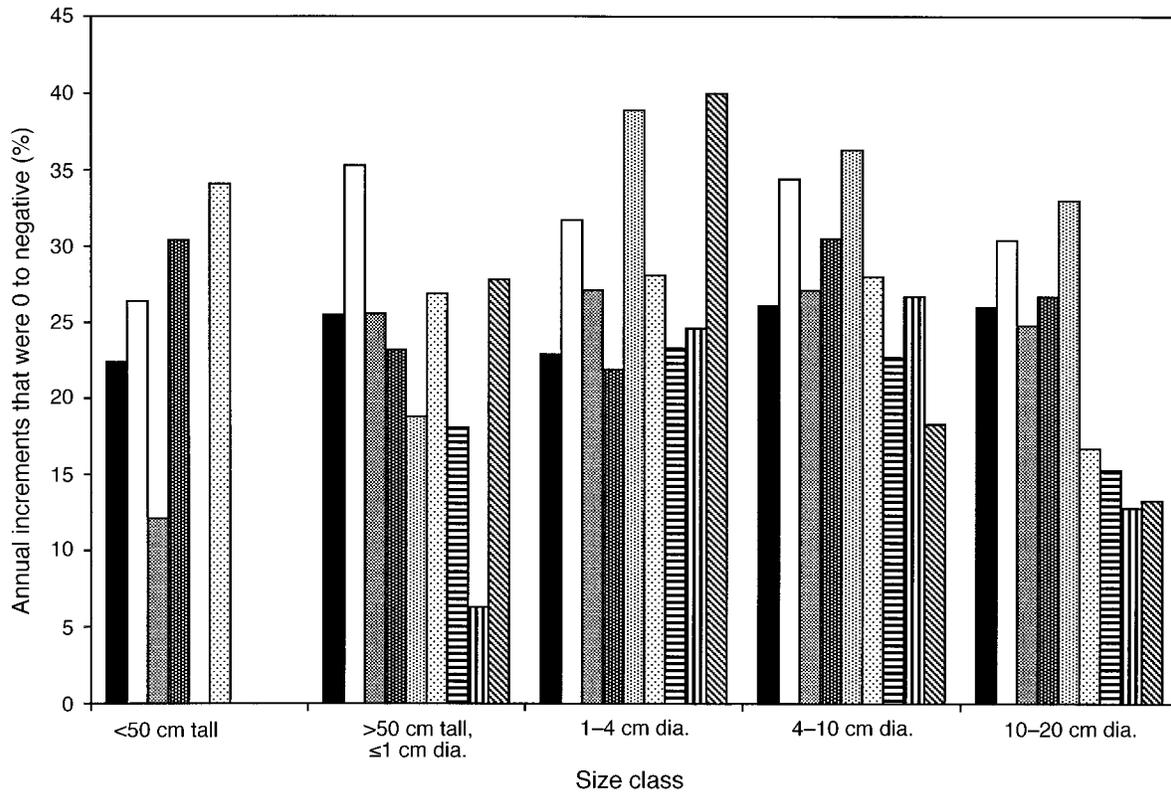
FIG. 2. Percentage of 1-yr height increments that were zero or negative, by species and juvenile size class. For each size class, species are, from left to right: *Minquartia, Lecythis, Hymenolobium, Dipteryx, Hyeronima, Balizia, Simarouba, Cecropia insignis,* and *C. obtusifolia.* Data are given for species/size classes with samples of ≥10 annual increments. Sample sizes (number of increments) for the nine species are, respectively: <50 cm tall—143, 87, 58, 23, . . . , 138, . . . , . . . , . . . ; ≤1 cm diameter—714, 442, 78, 651, 16, 283, 331, 16, 18; >1–4 cm diameter—1082, 993, 317, 365, 126, 398, 580, 65, 45; >4–10 cm diameter—1128, 541, 251, 128, 223, 446, 384, 90, 60; >10–20 cm diameter—331, 184, 113, 15, 109, 90, 137, 47, 15.

unmeasured because they grew out of measuring height range. Even considering these caveats, however, several interesting trends can be seen.

Based on this analysis (Table 5), passage times to grow from 50 cm tall to the 10 cm diameter pole stage for nearly all of these species are unlikely to be less than 20 yr, and may be considerably longer. When estimated from the greatest observed net height growth over periods of different length, the passage time estimates increase markedly with increasing interval length, from 5 to 15 yr (and, in the case of *Minquartia,* with no substantive change in sample sizes). This suggests that the faster height growth rates that these species can maintain over shorter periods (e.g., Table 2) are unlikely to be sustainable over the actual time period taken to reach 10 cm in diameter. These passage times may be overestimated for species represented by few individuals (as for the *Cecropia* species generally, and for several species over 15-yr intervals). Nevertheless, the well-represented species, such as *Minquartia* and *Lecythis,* with 24–71 individuals per size class observed for 15 yr (Table 5c), indicate that at least some of the slower growing canopy species are

likely to take >30–50 yr to reach even the lower sub-canopy.

DISCUSSION

Height growth capacity of tropical canopy trees

The large samples of increments from this long-term study have provided a way to assess height growth potential during regeneration for diverse tree species in tropical rain forest at La Selva, Costa Rica. By accumulating height growth records from many individuals, from many years and thus from varied climatic conditions, and over a broad range of microsite conditions, we have a robust estimate of the maximum potential of these species for height growth up to the subcanopy in the old-growth forest.

We used two approaches to assess the "factor-ceiling distribution" (Thomson et al. 1996) of annual height increments for these species in each juvenile size class: the top increment ever observed, and the mean of the top five increments. Both of these measures demonstrate three clear patterns. First, all of these species show substantial ontogenetic increases in their capacity

TABLE 3. Setbacks in height growth during regeneration.

Species	Percentage of individuals with ≥1 annual increment				Greatest annual height loss (cm)	Trees (N)
	≤0 cm	≤−25 cm	≤−50 cm	≤−100 cm		
≥50 cm tall, ≤1 cm diameter						
Minquartia	86.4	31.8	11.4	2.3	−180	44
Lecythis	97.0	54.5	39.4	12.1	−178	33
Hymenolobium	87.5	75.0	50.0	25.0	−205	8
Dipteryx	91.4	42.9	28.6	2.9	−140	35
Balizia	75.0	41.7	33.3	8.3	−166	12
Simarouba	78.6	35.7	14.3	0.0	−85	14
1–4 cm diameter						
Minquartia	94.6	56.8	35.1	16.2	−436	37
Lecythis	100.0	58.7	34.8	26.1	−353	46
Hymenolobium	94.1	76.5	52.9	35.3	−426	17
Dipteryx	84.6	46.2	15.4	0.0	−65	13
Hyeronima	100.0	100.0	80.0	80.0	−409	5
Balizia	100.0	83.3	66.7	61.1	−482	18
Simarouba	85.4	56.1	36.6	26.8	−561	41
4–10 cm diameter						
Minquartia	100.0	92.9	57.1	21.4	−628	14
Lecythis	100.0	88.2	52.9	29.4	−1079	17
Hymenolobium	85.7	78.6	64.3	35.7	−731	14
Dipteryx	100.0	100.0	80.0	40.0	−207	5
Hyeronima	100.0	100.0	88.9	66.7	−895	9
Balizia	96.2	69.2	46.2	30.8	−322	26
Simarouba	60.9	43.5	30.4	26.1	−486	23
10–20 cm diameter						
Minquartia	80.0	80.0	80.0	60.0	−207	5
Lecythis	66.7	50.0	50.0	16.7	−350	6
Hymenolobium	100.0	83.3	83.3	50.0	−251	6
Hyeronima	62.5	62.5	62.5	25.0	−1334	8
Simarouba	33.3	16.7	16.7	16.7	−122	6

Notes: For trees with 10 consecutive years of measured height increments, data are the percentages of individuals having at least one annual height increment that was zero or negative during the 10 years and the greatest observed annual height loss in these 10-yr records, for each species/size cohort. Data are for cohorts with $N \geq 5$ trees.

for height growth. Secondly, the two pioneer species (*Cecropia*) differ from the nonpioneers in two ways: by being able to grow 1 m or more in height in the smallest juvenile size class, and by their decline in height growth capacity at reaching the large pole stage (10–20 cm diameter). Thirdly, *Simarouba* is distinguished from the other nonpioneers by its higher potential height growth rates through regeneration.

Our data show that all of these species are capable of growing 1–3 m in height in a year, through most juvenile stages, in old-growth forest at La Selva. An interesting comparison can be made with the performance of four of these species when grown in plantations adjacent to the La Selva forest (Butterfield 1995). As might be expected, three of them showed rapid net height growth under plantation conditions; their average heights 3 yr after being planted out as small seedlings were: *Dipteryx*, 4.8 m (1.6 m/yr); *Hyeronima*, 5.4 m (1.8 m/yr); and *Simarouba*, 6.4 m (2.1 m/yr). *Minquartia,* however, which shows severe leaf damage and low survival in full sun (Butterfield 1995), had higher (maximum) growth rates in the forest (Table

2) than in the plantation (average 3-yr height of 1.3 m, or growth of 0.4 m/yr; Butterfield 1995).

Ecological implications of means vs. maxima

The very low averages for annual height increments for most of the study species in most juvenile size classes underline the great difference between mean and maximum growth rates for young trees in this forest. Although all nine species are capable of large annual height increments, their mean growth rates at all juvenile sizes are much lower. The path of upward growth to the canopy is clearly not a straight one in most cases. As demonstrated by the 10-yr records (Table 3) and by the decreased maximum net height increments with longer time intervals (Tables 2 and 5), juvenile trees of these species repeatedly suffer major stem breakage and height loss, and frequently experience periods of no net height growth (as found for small saplings of *Pourouma bicolor* [Cecropiaceae] at La Selva; King 1993). A practical consequence of this distinction between mean and potential growth rates is that, for projecting the potential growth performance
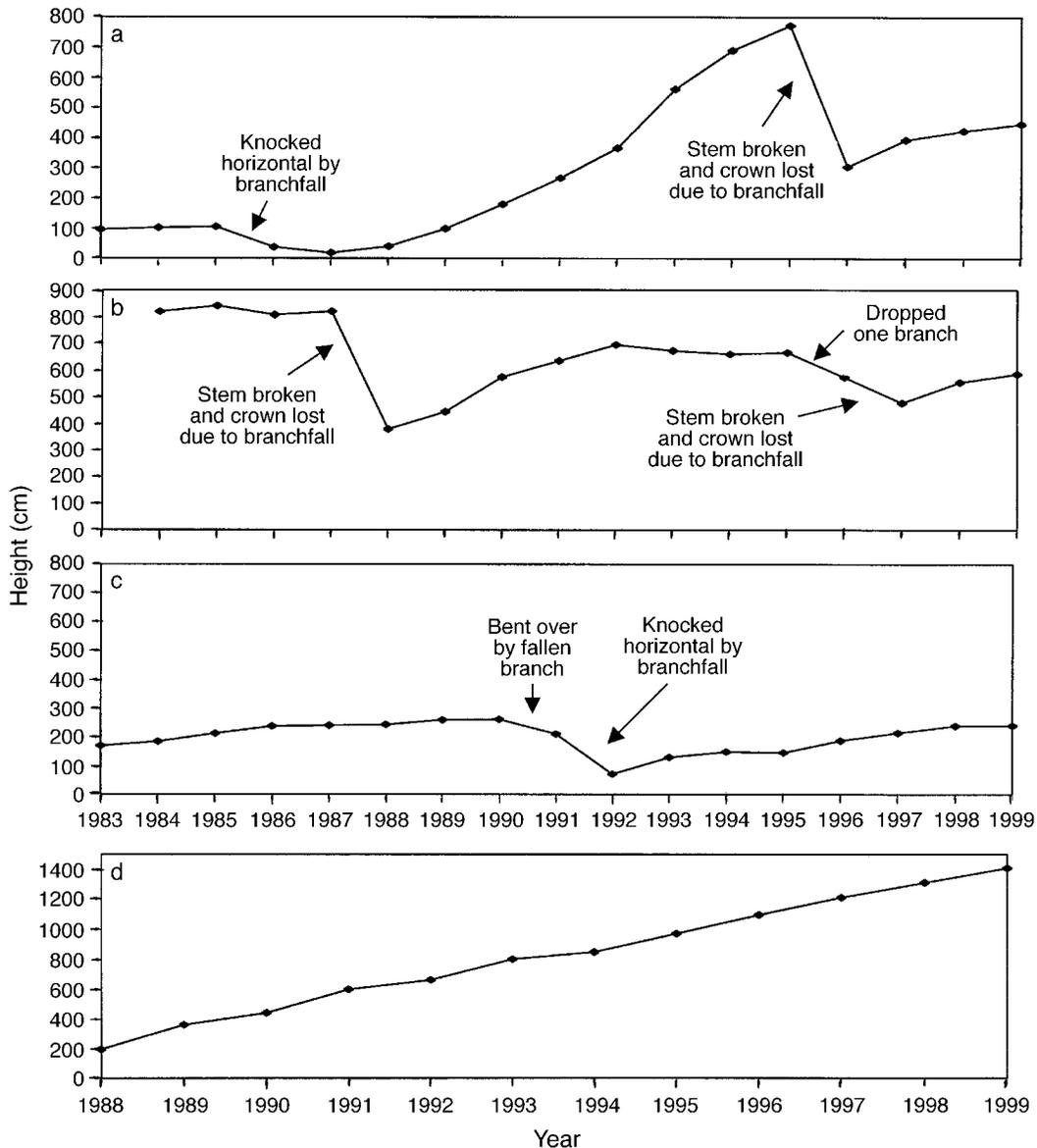
FIG. 3. Setbacks from physical damage during long-term height growth trajectories of three juvenile canopy trees, compared to the top long-term height growth record in the data set (note that axes differ among panels). (a) *Balizia* #3074: no net height growth during 6 yr as a small sapling, then a major postgap growth spurt that was largely annulled by stem breakage and crown loss (net height loss = 467 cm). (b) *Minquartia* #5055: height reduced by half (−441 cm) by a branchfall, followed by loss of half the height gain of the next 4 yr through further crown damage (−92 cm from losing one branch, −96 cm from losing the entire remaining crown). (c) *Dipteryx* #99155: gradual growth over 7 yr (95 cm total increment), which was negated when the sapling was flattened by a branchfall (zero net height growth in the last 12 yr). (d) *Simarouba* #2017: the record long-term (≥10 yr) height gain among all juveniles in the study (110 cm/yr over 11 yr), with no setbacks from physical damage.

of tropical rain forest tree species in plantations, potential growth, as assayed by observed maximum growth rates, would be much more useful than the mean growth rates of juveniles in old-growth forest.

The erratic upward path shown by our study trees at La Selva is likely to be characteristic of tree saplings in many forests. Pacala et al. (1994) found similarly complex patterns of height growth for small saplings

in temperate deciduous forest. If they are to be realistic, forest dynamics models will have to be designed to take this into account.

How long does successful regeneration actually take for tropical canopy trees?—Short of following individual juvenile trees all the way up to the canopy, the only way to estimate the time involved in the regeneration of these trees is to use observed growth rates

TABLE 4. Maximum height observed for each of nine focal tree species in three diameter size classes (sample sizes are as in Table 2).

	Maximum height (cm) by size class		
Species	≥50 cm tall, <1 cm diameter	1–4 cm diameter	4–10 cm diameter
Minquartia	242	869	1663
Lecythis	303	903	1580
Hymenolobium	258	829	1677
Dipteryx	292	1070	1685
Hyeronima	168	808	1524
Balizia	297	786	1670
Simarouba	258	757	1693
Cecropia insignis	220	817	1480
C. obtusifolia	200	714	1415

to project the time required to pass through each of the juvenile size classes. The differences between these species' height growth potential and their actual mean growth rates, however, translate into large differences in projected passage times. Given the evidence for a high incidence of periods with zero or negative height growth for these juvenile trees, even those that have survived over periods of 10–15 yr, the strong declines in maximum height increments with length of interval, the lack of temporal autocorrelation in juvenile height growth, and our estimates of the time required to reach even 10 cm in diameter (Table 5), it seems likely that the nonpioneer species will take considerably more than 50–60 yr to grow to the canopy (diameters of ~30 cm for most species; Clark and Clark 1992). Such time periods are in the range predicted from an earlier analysis of passage time (Clark and Clark 1992) for six of these species through ontogeny to canopy-sized adults. Passage times to 30 cm diameter, based on maximum and median 4-yr diameter increments, respectively, are: *Lecythis*, 59 and 462 yr; *Minquartia*, 38 and 186 yr; *Hymenolobium*, 53 and 210 yr; *Dipteryx*, 46 and 177 yr; *Balizia*, 38 and 204 yr; *Hyeronima*, 34 and 253 yr.

Height growth patterns and tree functional groups

In a previous analysis of the diameter growth patterns of these trees through life history (Clark and Clark

TABLE 5. Estimated minimum passage times for saplings to grow from 50 cm tall and <1 cm diameter to 10 cm diameter for the nine focal tree species, based on the maximum net height increments observed over 5-, 10-, and 15-yr periods (a–c, respectively).

	Size class										Estimated no. yr to reach 10 cm diameter
	≥50 cm tall, <1 cm diameter			1–4 cm diameter			4–10 cm diameter				
Species	Years	Max (cm)	(N)	Years	Max (cm)	(N)	Years	Max (cm)	(N)	Out of range† (%)	
a) Observations over 5-yr period											
Minquartia	5.1	189	100	8.1	385	71	8.2	483	74	2.6	21.4
Lecythis	8.8	143	50	13.8	217	56	8.0	425	43	2.3	30.6
Hymenolobium	3.1	336	10	17.8	160	26	11.7	361	18	14.3	32.7
Dipteryx	4.2	290	74	10.5	372	18	11.4	270	8	20.0	26.0
Hyeronima	1.8	327	2	6.3	507	14	10.8	330	20	9.1	19.0
Balizia	4.6	266	36	5.7	429	38	9.4	468	38	0.0	19.8
Simarouba	1.7	604	41	2.8	890	52	6.1	773	42	12.5	10.6
Cecropia insignis	1.6	541	2	2.4	1262	8	3.4	988	7	12.5	7.3
C. obtusifolia	...	...	...	7.8	328	1	7.6	460	4	60.0	>15.4
b) Observations over 10-yr period											
Minquartia	5.8	332	45	12.9	485	69	11.7	681	73	3.9	30.4
Lecythis	10.8	235	35	15.5	388	51	17.9	379	33	2.9	44.1
Hymenolobium	8.2	255	8	8.8	651	21	10.4	819	19	9.5	27.3
Dipteryx	6.4	377	41	14.8	525	14	17.8	345	7	22.2	39.1
Hyeronima	3.9	303	2	29.8	215	7	12.1	590	17	15.0	45.8
Balizia	5.3	464	13	8.5	575	26	8.8	1003	31	3.1	22.6
Simarouba	1.9	1117	14	4.8	1040	40	11.9	785	17	43.3	18.6
Cecropia insignis	12.8	133	1	6.0	1001	1	...	−621	2	33.3	>18.8
C. obtusifolia	...	...	...	...	...	...	13.1	536	1	50.0	>13.1
c) Observations over 15-yr period‡											
Minquartia	9.0	320	32	19.0	494	64	16.4	727	71	1.4	44.4
Lecythis	15.2	249	28	17.5	513	45	18.9	537	24	0.0	51.7
Hymenolobium	15.5	201	5	35.8	239	10	31.4	405	8	20.0	82.8
Dipteryx	11.7	309	11	18.1	645	6	9.5	969	6	0.0	39.4
Hyeronima	4.7	375	1	43.2	222	2	9.7	1111	10	0.0	57.6
Balizia	11.4	326	2	6.7	1093	8	18.6	713	6	0.0	36.7

Notes: Max, maximum observed net height increment over the period; *N,* number of measured increments. Ellipses indicate that data were not available.

† ''Out of range'' is the percentage of individuals in the size class for which the increment could not be determined because of growth beyond the measuring range.

‡ For the six species with measurements beginning in 1983.

1999), we found that the ontogenetic patterns of diameter growth capacity of these species correlated with their patterns of juvenile microsite occupancy (Clark and Clark 1992). Together, this suggested five ecological groups among the nine study species. Microsites were defined as ''gap'' (a vertical hole extending down to within 2 m of the ground), ''mature'' (with the top canopy at the level of the immediately surrounding forest), and ''building'' (intermediate between the two; Clark and Clark 1992). *Lecythis* and *Minquartia,* associated with darker, non-gap microsites through regeneration (microsite group A), showed consistently low capacity for diameter growth through all juvenile sizes. *Hymenolobium* and *Dipteryx*, characterized by increasing crown illumination and association with gap/building sites through ontogeny (microsite group B), showed very low diameter growth potential at the smallest juvenile sizes, but increased strongly in maximum diameter growth on reaching the subcanopy (diameters 10–20 cm). The two *Cecropia* spp. (microsite group D) showed high crown illumination and a strong association with gap/building microsites at all juvenile sizes, and they had the greatest diameter growth potential of all nine species as small saplings. *Balizia* and *Hyeronima* (microsite group C) had a very distinctive pattern of microsite occupancy: a strong association with gap/building sites as very small saplings and again as subcanopy trees, and their diameter growth capacity was intermediate between that of microsite groups B and D. Finally, *Simarouba* was anomalous; although it showed a group B pattern of microsite occupancy, its capacity for diameter growth was greater than that of all the other nonpioneers and, in fact, eclipsed that of the two *Cecropia* species in the larger juvenile sizes.

The patterns of height growth potential that we found in this study do not show as clear a correspondence with juvenile microsite patterns as we found with diameter growth. Although the ontogenetic patterns of relative height growth capacity of *Simarouba* and the two *Cecropia* species corresponded fairly well to those found with relative diameter growth potential, the nonpioneer species of microsite groups A–C (Table 1) were not distinguishable here in terms of their potential height growth rates. Diameter growth performance in old-growth forest conditions thus appears to be a more useful indicator than height growth for helping to identify functionally distinct groups of tropical trees.

Conclusions

These findings from a 16-yr study have revealed the complex nature of upward growth for young trees en route to the canopy in old-growth tropical rain forest. The data are, however, from only a relatively brief portion of the time scale of regeneration for most of these species. It is clear that determining the actual growth patterns that characterize successful regeneration for such trees will require continuing measurements for many more years. Secondly, for a robust understanding of the regeneration process of tropical rain forest trees, similar studies of height growth performance through ontogeny and through time are needed for many more tree species and in diverse tropical forests.

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