

Comparative Analysis of Microhabitat Utilization by Saplings of Nine Tree Species in Neotropical Rain Forest¹

David B. Clark, Deborah A. Clark

La Selva Biological Station, Organization for Tropical Studies, Apartado 676, San Pedro 2050, Costa Rica and

Paul M. Rich

Biological Sciences, University of Kansas, Lawrence, Kansas, 66045-2106, U.S.A.

ABSTRACT

We examined the hypothesis that tropical rain forest tree species differ significantly in the degree to which their regeneration is associated with treefall gaps. Using static and dynamic analyses, we evaluated crown light environments and forest structure around 0.5–5 m tall saplings ($N = 424$) of two pioneer and seven nonpioneer tree species in old growth tropical wet forest at the La Selva Biological Station, Costa Rica. Canopy photographs were taken with a fisheye lens directly above all individuals. Each photograph was analyzed to calculate a Global Site Factor (GSF), which is analogous to the percentage of photosynthetically active radiation reaching a site relative to a totally open site. The amount and directionality of crown illumination were also estimated visually using a crown position index (Dawkins & Field 1978, Clark & Clark 1992). Forest structure around each individual, a reflection of local disturbance history, was categorized as gap, building, or mature.

Saplings of all nine species were found in relatively dark sites (\bar{x} Global Site Factors 1.9–10.8%). The two pioneer species (*Cecropia*) were found in higher light microsites than the other species and were significantly different from each other. There were no significant differences in GSF among nonpioneer species. Results were similar for the direct and diffuse components of GSF, and for the crown position index. In contrast, forest structure around saplings varied significantly among nonpioneer species but not between *Cecropia* species.

For six of the nine species short-term height or diameter growth was correlated with GSF or its direct or diffuse components. GSF was weakly but significantly correlated with sapling height and crown position.

Analyses over time showed that all nine species had progressively lower crown illumination and fewer individuals in gap/building sites for 2–8 yr after initial encounter. Particularly steep decreases for *Hyeronima* and *Pithecellobium* saplings indicate that these species establish under canopy openings that subsequently fill in.

Canopy photography, crown position index, and the forest structure index all provided ecologically interpretable information. Only canopy photography distinguished between microsites of the two *Cecropia* species. Forest structure and crown position indices are rapid and inexpensive methods for obtaining long-term information on microhabitats around individual trees.

We found significant interspecific differentiation in microhabitat occupancy along a light gradient of only 0–25 percent of full sun. A crude 3-point index of forest structure revealed even further resolution. This study focused on only three microsite variables and a restricted size range of saplings. Comprehensive understanding of tropical tree regeneration will require long-term concurrent measurements of individual performance and associated environmental variables for all size classes of a broad range of species.

RESUMEN

Examinamos la hipótesis de que las especies de árboles de bosque tropical húmedo se diferencian significativamente en el grado de la relación entre su regeneración y claros naturales del bosque. Usando análisis estáticos y dinámicos, evaluamos los ambientes lumínicos de las copas y la estructura del bosque alrededor de arbolitos de 0.5–5 m de altura ($N = 424$) de dos especies pioneras y siete especies no-pioneras en bosque tropical muy húmedo de la Estación Biológica La Selva, Costa Rica. Tomamos fotografías del dosel con lente ojo de pez arriba de todos los individuos. Cada fotografía fue analizada para calcular un factor global de sitio (Global Site Factor = GSF), lo cual es análogo al porcentaje de radiación fotosintéticamente activa que llega a un sitio comparado con un sitio despejado. La cantidad y direccionalidad de la iluminación de la copa fueron estimadas visualmente usando el índice de posición de la copa (Dawkins & Field 1978, Clark & Clark 1992). La estructura del bosque alrededor de cada individuo, que refleja la historia local de perturbación, fue caracterizada como claro, maduro, o intermedio.

Arbolitos de todas las nueve especies ocurrieron en sitios relativamente oscuros (promedios de GSF 1.9–10.8%). Las dos pioneras (*Cecropia*) se encontraron en micrositios más iluminados que las demás especies, y eran diferentes

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entre ellas mismas. No habían diferencias significativas entre las especies no-pioneras. Los resultados eran similares para los análisis de los componentes directos e indirectos de GSF y para y el índice de posición de la copa. En cambio, la estructura del bosque alrededor de los arbolitos variaba significativamente entre las especies no-pioneras pero no entre las dos pioneras.

Para seis de las nueve especies el crecimiento a corto plazo en diámetro o altura fue correlacionado con GSF o su componente directo o indirecto. GSF fue débil pero significativamente correlacionado con la altura del arbolito y la posición de la copa.

Los análisis a través del tiempo demostraron que todas las especies tenían copas progresivamente menos iluminadas y con un menor porcentaje de individuos en micrositios de claro/intermedio en los 2 a 8 años después de que fueron encontrados. El cambio fue especialmente fuerte para arbolitos de *Hyeronima* y *Pithecellobium*, lo cual indica que éstas especies se establecen bajo aperturas en el dosel que después se cierran.

La fotografía de doseles con lente ojo de pez, los índices de la posición de la copa, y el de estructura de bosque, todos proporcionaron información que fue interpretable ecológicamente. Solo la fotografía distinguió entre los micrositios de bosque *Cecropia*. Los índices de estructura de bosque y posición de la copa son métodos rápidos y baratos para obtener información a largo plazo sobre los microambientes alrededor de árboles individuales.

Encontramos una diferenciación significativa entre las especies en cuanto a su ocupación de microambientes a lo largo de una gradiente de solo 0–25 por ciento de la luz de pleno sol. Un índice crudo de solo tres categorías de estructura de bosque proporcionó aún más resolución. Este estudio se enfocó en solo tres variables y en un ámbito restringido de tamaños. Para lograr un entendimiento comprensivo de la regeneración de árboles de bosques tropicales, será necesario medir concurrentemente la supervivencia, crecimiento y microambientes de individuos a largo plazo y para todos los tamaños de una variedad de especies.

Key words: Costa Rica; gaps; light environments; pioneers; saplings; tropical moist forest; tropical tree regeneration.

A CENTRAL PARADIGM OF TROPICAL TREE DEMOGRAPHY is that species differ significantly in the degree to which their regeneration is related to natural disturbances, particularly treefall gaps (see reviews by Hartshorn 1978; Whitmore 1984; Brokaw 1985, 1987; Clark & Clark 1987; Denslow 1987). In this paper, we assess the extent of such differences by analyzing microhabitats of small saplings of nine tropical wet forest tree species. The species (Table 1) range from pioneers (Swaine & Whitmore 1988) to species associated with nongap sites through ontogeny (Clark & Clark 1992). We expected to find significant differences between the pioneers and non-pioneers in their relations to light and disturbance. However, pioneer species typically account for only a small fraction of the tree species in any tropical rain forest. For understanding tropical tree regeneration, it is of special interest to determine the degree of difference between the nonpioneer species. Are there only a few "major life history guilds" (Hubbell & Foster 1986); or, are there in fact many ecologically distinguishable life history patterns?

There are two general approaches for evaluating tree regeneration processes. Static analyses are based on measuring saplings' microenvironments at a single time and using these "snapshots" to infer past and future events (*cf.* Brandani *et al.* 1988, Welden *et al.* 1991). A weakness of this approach is that it rests on currently available evidence. Events leaving no lasting record may be missed, and the significance of current conditions may be incorrectly interpreted. Far preferable are dynamic analyses: measuring performance and microhabitat for the

same individuals over time. This longer-term approach has proved useful for understanding factors affecting the regeneration of temperate zone trees, which serendipitously preserve a record of performance in their growth rings (*cf.* Canham 1985). For trees of tropical wet forests, where reliable annual growth rings are often absent and understory conditions can change rapidly following disturbance (Fetcher *et al.* 1985), studies combining simultaneous measurements of performance and microhabitat over time are few. Here we report results from both static and dynamic analyses of the regeneration process for nine tree species of tropical wet forest.

In this study we focus on saplings 0.5–5 m tall. Saplings of this size are usually ignored in forest inventory studies, which commonly concentrate on trees >10 cm in diameter (for recent examples see studies in Swaine & Lieberman 1987 and Gentry 1990). From the perspective of trying to understand factors affecting regeneration, studies of trees >10 cm DBH miss the vast majority of events that determine whether an individual plant survives to reach the canopy. At the other extreme, numerous studies have focused on seed germination and the factors affecting seedling establishment for tropical trees (*cf.* distance to adults, Clark & Clark 1984; seed/seedling predation, DeSteven & Putz 1984, Howe *et al.* 1985; pathogens, Augspurger 1984; physical damage, Clark & Clark 1991; light, Turner 1990). For small saplings, however, we know of only two published studies from tropical rain forests (Welden *et al.* 1991, Clark & Clark 1992) where environmental variables and individual performance

TABLE 1. The nine species of canopy and emergent trees for which sapling microsites were evaluated in old growth tropical wet forest at the La Selva Biological Station, Costa Rica. Reference vouchers in the Costa Rican National Herbarium are given in brackets.

Species	Canopy status as adult
<i>Dipteryx panamensis</i> (Pittier) Record & Mell (Papilionaceae) [R. Robles 1199]	Emergent
<i>Hyeronima alchorneoides</i> Alemaó ^a (Euphorbiaceae) [T. Chacón 751]	Emergent
<i>Hymenolobium mesoamericanum</i> Lima ^b (Papilionaceae) [R. Aguilar 19]	Emergent
<i>Lecythis ampla</i> Miers (Lecythidaceae) [R. Robles 2208]	Emergent
<i>Pithecellobium elegans</i> Ducke ^c (Mimosaceae) [B. Hammel 17319]	Emergent
<i>Minquartia guianensis</i> Aubl. (Olacaceae) [G. Herrera 2250]	Canopy
<i>Simarouba amara</i> Aubl. (Simaroubaceae) [R. Robles 1670]	Canopy
<i>Cecropia insignis</i> Liebm. (Cecropiaceae) [W. Burger 11135]	Canopy
<i>Cecropia obtusifolia</i> Bertol. (Cecropiaceae) [R. Robles 1446]	Canopy/Subcanopy

^a *Hyeronima oblonga* in Clark and Clark (1987).

^b *Hymenolobium pulcherrimum* in Clark and Clark (1987).

^c *Pithecellobium pedicellare* in Clark and Clark (1987), Oberbauer *et al.* (1989).

have been measured concurrently for at least several years (such studies are currently underway at several sites). The paucity of data is particularly notable, given the importance of the postestablishment, small juvenile stages for understanding tree regeneration (Wyatt-Smith 1987, Clark & Clark 1992).

An additional goal of this research was to compare different techniques for assessing microhabitats. Forest structure and understory light environments are complex variables. They can be described with techniques ranging from simple subjective indices to computer analysis of remote-sensed images. Here we evaluate the ecological information provided by three methods that vary greatly in cost and ease of application.

METHODS

The study was carried out in old growth lowland forest at the La Selva Biological Station in the Atlantic lowlands of Costa Rica (10°26'N, 84°00'W). The forest has been classified as Tropical Wet Forest in the Holdridge Life Zone system (Hartshorn 1983). Rainfall averages *ca* 3900 mm/yr, with no month averaging <100 mm; temperature averages 26°C (OTS unpublished records).

The demographic data reported here are from a long-term, landscape-scale study of canopy tree

regeneration at La Selva. Results from the first 6 yr and a detailed description of sampling and measurement protocols are given in Clark and Clark (1992). A plotless sampling method was used to accumulate samples of saplings of the nine study species in an area of approximately 150 ha of old growth forest. Within size classes, the sampling protocols precluded bias with respect to individuals' vigor, form, or microhabitat variables (Clark & Clark 1992).

All saplings and their microsite variables were measured annually during 1983–91 (or from date of first encounter, if post-1983). Diameter was measured at a permanently marked site on the stem at 0 cm, 40 cm, or 130 cm from the ground, depending on the individual's height and stem form. Diameters <4 cm were measured with calipers, those ≥4 cm with a diameter tape. Height was measured with a folding ruler or a telescoping pole. Annualized growth rates were calculated by the formula $(\text{second measurement} - \text{first measurement}) / (\text{interval between measurements in days}) \times 365$. The extent and direction of crown illumination was evaluated using Dawkins and Field's (1978) crown position index: 1 = no direct light; 2 = crowns lit only from the side; 3 = partial (10–90%) vertical illumination; 4 = full vertical illumination; and 5 = crown fully exposed to vertical and lateral

TABLE 2. *Global Site Factor (an estimate of crown illumination, see Methods) for 0.5–5 m tall saplings of nine species of canopy trees at the La Selva Biological Station, Costa Rica. Species names are given in Table 1. Means followed by different letters are significantly different at $P < .05$ by Tukey's pairwise comparison of means.*

Species	Global Site Factor			
	Mean	Range	CV	(N)
<i>C. obtusifolia</i>	10.8 ^a	1.6–24.8	58.0	(31)
<i>C. insignis</i>	5.6 ^b	0.4–16.4	72.0	(18)
<i>Hieronima</i>	2.4 ^c	1.2– 6.4	66.7	(9)
<i>Pithecellobium</i>	2.2 ^c	0.6–10.7	80.2	(43)
<i>Simarouba</i>	1.9 ^c	0.4– 6.8	66.4	(91)
<i>Hymenolobium</i>	2.4 ^c	0.7–10.2	92.9	(16)
<i>Dipteryx</i>	1.9 ^c	0.7– 4.9	43.9	(73)
<i>Lecythis</i>	1.9 ^c	0.7– 7.9	58.3	(70)
<i>Miquartia</i>	1.9 ^c	0.5– 7.4	67.3	(73)

light. Crowns lit only from the side (lateral light, class 2) were subdivided into high (exposed to at least one major or multiple medium-sized openings), low (no large or medium openings), and intermediate categories (Clark & Clark 1987, 1992). Forest structure at each individual's location was evaluated using a 3-category index. Sites open vertically to the sky with no vegetation taller than 2 m were classified as gaps (Brokaw 1982). Sites with maximum vegetation height equal to or greater than the mean forest canopy height were classified as mature phase. Intermediate sites were classified as building phase (Whitmore 1984). For all analyses we combined gap and building phase individuals in one category.

The data for static analyses of microsites included all 0.5–5 m tall saplings in the long-term study that were alive between August 1990 and January 1991 (a few saplings in a remote section of La Selva were excluded). Crown light environments were evaluated using the crown position index and fisheye photographs. A photograph was taken immediately above each sapling using a 35 mm camera with a Nikkor 8 mm hemispherical lens mounted in a gimbal for self-leveling. The gimbals were raised on a monopod to the highest point of the crown. Photographic negatives (Kodak Tri-X 400 ASA film) were analyzed using the computer program CANOPY (Rich 1990). Direct site factor (DIRsf: the proportion of direct light potentially reaching a site relative to a site in the open) and diffuse site factor (DIFsf: the proportion of diffuse light potentially reaching a site relative to a site in the open) were calculated based on the intersection

of the sun's track with canopy openings (Rich 1990). Each photograph was analyzed repeatedly until the difference between successive DIRsf estimates was ≤ 0.5 percent. Global Site Factor (GSF), which is analogous to the percentage of photosynthetically active radiation (PAR) reaching a site relative to a totally open site, was calculated using the equation $GSF = (0.45 \times DIRsf) + (0.55 \times DIFsf)$. These weightings lead to GSF values which are highly correlated with long-term measurements of photosynthetically active radiation (PAR) in the understory at La Selva (Rich *et al.*, 1993). To examine the relation of static microhabitat variables to short-term growth, we measured height and diameter of individuals in the static sample between January and June 1989 and again between August 1990 and January 1991. Average time between remeasurements was 573 days. Canopy photographs were taken and crown position index was evaluated at the time of remeasurement.

To examine microhabitat dynamics, we analyzed successive annual microhabitat measurements for all saplings that were 0.5–5 m tall at time of first encounter. For crown position these data include all saplings in the initial 1983 sample (Clark & Clark 1992), as well as all saplings added over the subsequent 8 yr of study; forest phase measurements were begun in 1984.

RESULTS

RELATIONS OF SPECIES TO STATIC MICROHABITAT VARIABLES.—Global Site Factors (Table 2) differed significantly among saplings of the nine species (Kruskal-Wallis nonparametric ANOVA, $P < 0.0001$). The differences were due entirely to the two *Cecropia* species, whose means were 2–5 times higher than those of the other seven species. Mean GSFs of the seven nonpioneer species were extremely similar (1.9–2.4%, Kruskal-Wallis ANOVA among species, $P = 0.66$). The two *Cecropia* species, however, differed significantly between themselves (Mann-Whitney U , $P < 0.004$). *C. obtusifolia* saplings occurred in sites averaging almost twice the GSF of *C. insignis* (Table 2). DIRsf and DIFsf values followed the same pattern as GSF within and among species (data not shown).

Interspecific patterns of sapling crown positions were similar to those for GSF (Fig. 1). There were highly significant differences among the nine species (Kruskal-Wallis $P < 0.001$, $N = 424$). The two *Cecropia* species had the highest average crown positions, but did not differ significantly between themselves (Mann-Whitney $P = 0.09$). Among the

seven nonpioneer species crown positions were not significantly different (Kruskal-Wallis $P = 0.46$, $N = 375$).

The nine species differed greatly in the percentage of their saplings occurring in gap or building phase forest (Fig. 1; $\chi^2 = 30.94$, $P = 0.0001$, $df = 8$). However, the pattern was different than that shown by crown light environments. The non-*Cecropia* species differed significantly among themselves in the percentage of saplings in gap or building sites ($\chi^2 = 23.25$, $P < .001$, $df = 6$), while the two *Cecropia* species did not differ from each other ($\chi^2 = .25$, $P > 0.24$, $df = 1$).

RELATION OF PLANT HEIGHT AND GROWTH TO MICROHABITAT VARIABLES.—For all species combined, GSF was weakly related to sapling height ($r_s = 0.09$, $P < 0.05$, $N = 424$). Within species GSF was significantly correlated with sapling height only for *Dipteryx* and *Simarouba* ($r_s = 0.19$ and 0.31 , $P < 0.05$ and < 0.01 , $N = 73$ and 91 , respectively).

Because site factors were positively correlated with height, we used partial correlation controlling for individuals' height to examine the relation of growth to site factors (Table 3). All 18 partial correlations of direct and diffuse site factors with diameter growth were positive (8 significantly), suggesting that diameter growth was frequently light limited in the microhabitats where these saplings were growing. Direct site factor was an equal or better predictor of diameter growth than diffuse site factor for all 9 species. There was no clear difference between direct and diffuse site factors as predictors of height growth.

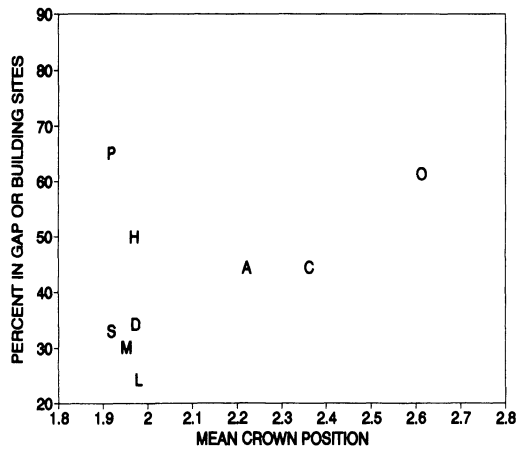


FIGURE 1. Percentage of each species' saplings that were in gap or building sites when first sampled, and mean crown position for the nine species. Sample sizes are as in Table 2. Letters are first letters of the genus names in Table 1 except A = *Hyeronima alchorneoides*, C = *Cecropia insignis*, and O = *Cecropia obtusifolia*.

RELATIONS BETWEEN MICROHABITAT VARIABLES.—For all species combined ($N = 424$ saplings), GSF and crown position were significantly correlated, but a linear model accounted for only a third of the variance ($r^2 = 0.34$, $P < 0.0005$). Median GSFs at low, medium, and high side light, and partial or full overhead illumination were 1.4, 1.7, 4.5, and 10.4 ($N = 78, 272, 56$, and 18). For the combined sample, crown position and GSF of saplings in gap or building-phase microsities were not different from those of individuals under mature forest canopy

TABLE 3. Partial correlations (controlling for sapling height; see text) between annualized diameter growth, annualized height growth, and three indices of light availability: Direct Site Factor (DIRsf), Diffuse Site Factor (DIFsf), and Global Site Factor (GSF) (see Methods), for saplings of the nine study species. Individuals with height decreases greater than the precision of measurement (i.e. >7%, Clark and Clark 1992) were not included.

Species	Partial correlation between annual Diameter growth				Partial correlation between annual Height growth			
	DIRsf	and DIFsf	GSF	(N)	DIRsf	and DIFsf	GSF	(N)
<i>C. obtusifolia</i>	0.49	0.33	0.48	(5)	-0.13	0.46	0.02	(5)
<i>C. insignis</i>	0.81*	0.39	0.78	(6)	0.61	0.76	0.65	(6)
<i>Hyeronima</i>	0.14	0.14	0.16	(8)	0.42	0.56	0.46	(6)
<i>Pithecellobium</i>	0.54**	0.35*	0.60***	(33)	0.74***	0.56***	0.76***	(34)
<i>Simarouba</i>	0.55***	0.28**	0.49***	(83)	0.44***	0.34***	0.44***	(86)
<i>Hymenolobium</i>	0.27	0.09	0.20	(15)	0.15	0.19	0.15	(11)
<i>Dipteryx</i>	0.10	0.07	0.11	(64)	0.08	0.22*	0.16	(63)
<i>Lecythis</i>	0.24*	0.17	0.24*	(62)	0.27*	0.15	0.24*	(61)
<i>Minquartia</i>	0.34**	0.31**	0.34**	(69)	0.16	0.06	0.13	(68)

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

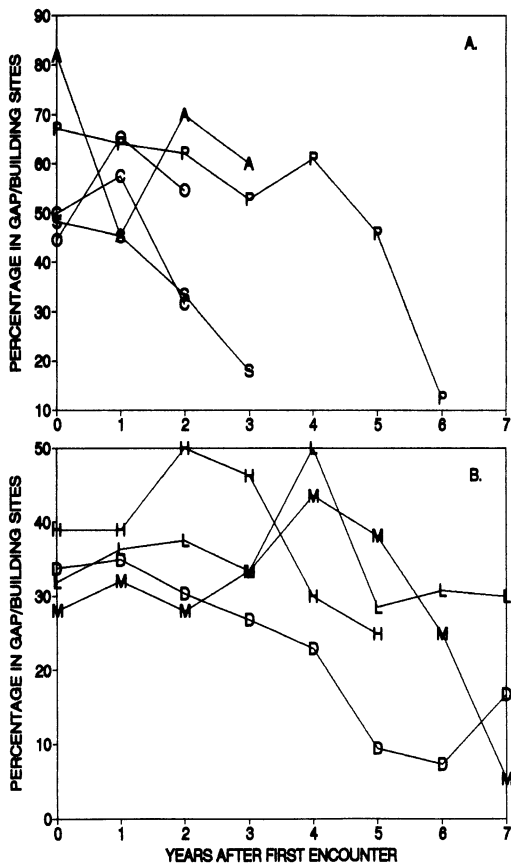


FIGURE 2. Trends through time in the percentage occurrence of all saplings in the long-term sample in gap or building sites. Only samples with >5 individuals are shown. Letters correspond to genus names (Table 1) except A = *Hyeronima alchorneoides*, C = *Cecropia insignis*, and O = *Cecropia obtusifolia*. (A) Species with >40% of their saplings in gap/building sites at first encounter. (B) Species with <40% of their saplings in gap/building sites at first encounter. Note different scales between graphs.

(Mann-Whitney U : crown position, $P = 0.79$; GSF, $P = 0.28$).

For the whole sample, DIRsf and DIFsf were significantly correlated ($r^2 = 0.656$, $N = 424$). However, at higher light levels there was in fact no significant relation between site factors. For DIRsf > 10, for example, DIRsf and DIFsf were not correlated ($r^2 = 0.03$, $P = 0.20$, $N = 24$).

SAPLING MICROSITES OVER TIME.—The static microsite data provide a point-in-time view of sapling crown light environments and their relation to forest structure. If, however, microenvironments change over time differentially among species, such data may

lead to erroneous interpretations of regeneration patterns. In the present study, the ages of saplings were unknown and may have differed between species. *Simarouba* and the two *Cecropia* species were first added to the long-term demography study in 1988; the average time that individuals in these species have been measured is therefore <3 yr. In contrast, all individuals of *Lecythis* and *Minquartia* were first measured in 1983 and 1984, and therefore averaged around 8 yr under study. The other species fall in between.

A reasonable hypothesis is that the crown light environments of surviving individuals should increase over time, as saplings grow taller and individuals in darker microsites die. On the scale of time and size used in this study, such a trend was not evident for any species (Figs. 2 and 3). In fact, all nine species had lower mean crown positions at the end of the study period than at the beginning. This represents an interval of 8 yr for *Dipteryx*, *Minquartia*, *Lecythis*, and *Hymenolobium*; 6 yr for *Pithecellobium*; 3 yr for *Simarouba* and *Hyeronima*; and 2 yr for the *Cecropia* species. The decline was particularly notable in *Hyeronima*, *Pithecellobium*, and *Simarouba*, the species with the highest initial crown positions among the nonpioneer species.

DISCUSSION

GENERAL PATTERNS OF TROPICAL RAIN FOREST TREE REGENERATION.—These data lead to several insights about tree regeneration in old growth tropical moist forest. Previously (Clark & Clark 1992) we showed that performance and static microhabitat distributions of small saplings were not good predictors of the behavior of large saplings or adults. The data of the present study show that there are substantial temporal shifts even for small saplings. Had we included the seed/small seedling stages, the shifts would probably have been even more dramatic. An additional consideration is that the size range of saplings analyzed was limited principally by the difficulty of raising the camera above taller individuals. We analyzed each species as if the 0.5–5 m tall class had a coherent biological meaning, and that this meaning was similar among species. Both of these assumptions need to be addressed in studies with larger sample sizes and across broader size intervals.

As expected, pioneer and nonpioneer species differed significantly in crown light environments. However, we believe that the more significant finding was that mean GSFs for saplings of all nine species ranged only from 2 to 11 percent. Even the

maximum values for the pioneer species *Cecropia obtusifolia* reached only 25 percent. Previous studies (La Selva: Chazdon 1986; Oberbauer *et al.* 1988, 1989; Barton *et al.* 1989; Denslow *et al.* 1990; King 1991; Panama: Howe 1990; Australia: Turton 1988; Malaysia: Turner 1990) have also shown that almost all tropical rain forest understory light environments fall within this range. The events influencing the regeneration of the vast majority of tropical rain forest tree species therefore occur over a very restricted range of light environments.

Even over this small gradient, however, the two *Cecropia* species in this study were clearly distinguished from the seven nonpioneer species by the canopy photography analysis. Equally notable was the relatively small but highly significant difference between the two *Cecropia* species: mean sapling GSFs of 6 percent GSF for *C. insignis* vs 11 percent GSF for *C. obtusifolia*. It seems likely that these species use gaps in old growth forest differentially. *C. obtusifolia* saplings may occur in larger gaps than *C. insignis* saplings, and/or in more highly illuminated sectors of gaps. A similar situation was reported by Brokaw (1987), who noted that three species of pioneer trees in Panama occurred in different sized gaps; although light environments were not measured, it seems likely that these species also differed in average crown lighting.

The prevalence of significant correlations between growth and crown light environments indicates that light is frequently growth-limiting for saplings of all of these species in old growth forests. The generality of growth/light environment correlations was especially notable considering the relatively short growth period measured and the small range of light environments occupied by the saplings. Similar evidence has been presented for other woody species in tropical rain forest understories (trees: Turner 1990, King 1991, Clark & Clark 1992; palms: Chazdon 1986; shrubs: Denslow *et al.* 1990, Levey 1990; cycads: Clark & Clark 1988). It is clear that the growth of the majority of tropical rain forest understory plants is limited by light. Although it was barely detectable in these data, light availability in general must increase with increasing plant height. A major and unresolved question is if light limitation ceases to be a measurable influence at some height.

Another unresolved issue is how or whether to infer life history patterns from individuals' microhabitat characteristics. For saplings of our study species at La Selva, death rates are high over the 0.5–5 m tall size range (see Clark & Clark 1992, diameter classes < 1 cm and 1–4 cm). For some of

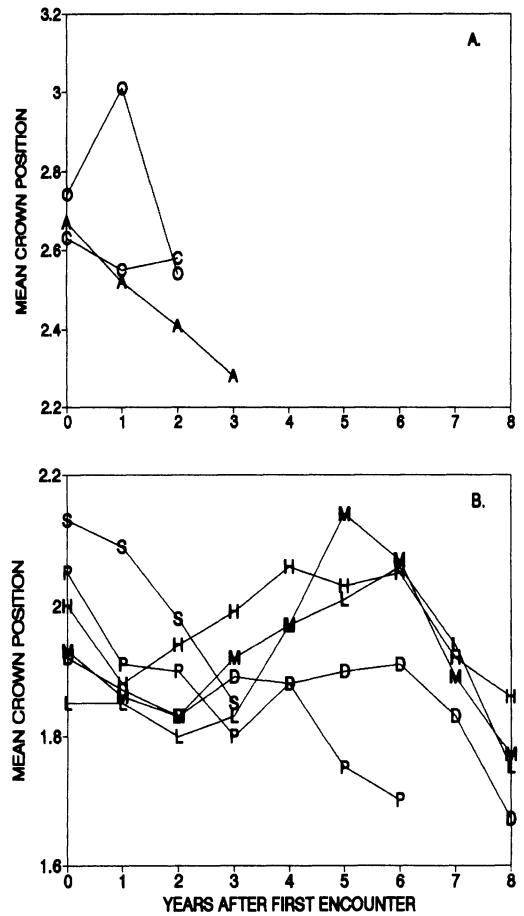


FIGURE 3. Trends through time in mean crown position index (see Methods) for saplings in the long-term sample. Letters correspond to genus names in Table 1 except A = *Hyeronima alchorneoides*, C = *Cecropia insignis*, and O = *Cecropia obtusifolia*. (A) Species with mean crown positions averaging greater than high lateral light (crown position > 2.5) at first encounter. (B) Species with mean crown positions initially averaging less than high lateral lighting (crown positions \leq 2.5). Note different scales between graphs.

these species, 6 yr survivorship of saplings was higher in microsites of higher irradiance. One possibility is that saplings in darker microsites are currently alive but their overall condition is declining, such that without a subsequent increase in light they will die. On the other hand, the tremendous dynamism of tropical wet forest (reviewed in Brokaw 1985 and Clark 1990) makes it likely that higher light environments will be created around saplings fairly frequently. Given the growth and death rates of these species, long-term data are needed to analyze this process.

INTERSPECIFIC COMPARISONS.—In previous work (Clark & Clark 1992) we have shown that relative growth and mortality rates varied substantially among six of the study species, and that these rates also varied through ontogeny. We distinguished four heuristic life history groupings based on growth, survival, and microhabitat occupancy of the species through all postestablishment, precanopy life stages (based on diameter class). We used letters to name the groups to avoid the nonoperational definitions commonly used to describe rain forest tree regeneration patterns.

Group A species (*Lecythis* and *Minquartia*) were defined as those that established in low light microsites, usually under mature phase forest, and occupied the relatively darkest, least disturbed microsites at all juvenile stages. Group B species (*Dipteryx*, *Hymenolobium*, and *Simarouba*) were distinguished by steady size-dependent increases in crown position and growth rates. Group C species (*Pithecellobium* and *Hyeronima*) were closely linked to disturbance at the germination/establishment stage but not at larger juvenile sizes. Group D was comprised of the two pioneers, *C. insignis* and *C. obtusifolia*, which had the highest crown light environments through ontogeny.

How do results from the current study compare with these previous results? In this study, which covered a much smaller size range, no obvious distinctions were observed between saplings of the group A and B species. Group B species' small saplings were initially found more frequently in gap/building microsites (Fig. 1), but this difference from Group A was relatively short-lived (Fig. 2). Saplings of Group C species showed a rapid decline through time in both crown light environment and percentage occurrence in gap/building sites. This is consistent with an early requirement of high-light sites for germination and/or establishment, followed by subsequent overtopping of the gap. The Group D (pioneer) species had the highest sapling crown light environments. Only about 50 percent of their small saplings were initially found in gap/building habitats (Fig. 3), but sapling crown position for both species was high relative to the other species. We think this indicates the importance of gap-edge habitat for these species. Although there are only 2 yr of successive measurements for these species, it appears that they may maintain high crown light environments throughout regeneration. This separates them from the group C species, both of which showed substantial declines in crown position and gap affinity over periods of 3 yr (*Hyeronima*) and 6 yr (*Pithecellobium*).

THE IMPORTANCE OF METHODS.—The crown position index and canopy photography methods of assessing sapling light microsites gave somewhat different results. Although both separated the pioneers from nonpioneers, only the canopy photographs clearly distinguished between the two *Cecropia* species. We expected Global Site Factor to be a more sensitive technique, in part because GSF is essentially a continuous variable, while Crown Position Index has only a few discrete values.

Canopy photographs provide objective, permanent, quantitative evaluations of light microsites. They can be reanalyzed at any time and under different assumptions. When the analyses are properly calibrated, they have the advantage of producing easily interpretable units. On the other hand, obtaining and analyzing canopy photographs is labor intensive, especially as plant height increases. High contrast, reflection-free photographs can only be taken under uniformly cloudy conditions, which poses a substantial logistical constraint. There are numerous possibilities for experimental error in all steps, from taking the photograph to its analysis (Rich 1990). Given the very low mean GSF values for the nonpioneer species in this study (1.9–2.4%), even small methodological errors may introduce considerable noise. Our photo analysis criterion was that repeated analyses of DIRsf for an image fall within ± 0.5 percent, a range equal to about 50 percent of the GSF means. However, the relative importance of this type of error decreases rapidly with increasing light.

Global Site Factor is an estimate of the percentage of photosynthetically active radiation (PAR) reaching a site compared to that reaching a fully exposed site. We used the program CANOPY (Rich 1990) to calculate each site's average GSF for a 1 yr period. Ultimately the only way to determine the correspondence of these GSF values to actual percent annual full sun PAR is to have long-term PAR data for the sites where photographs are taken. Taking yearlong PAR data over hundreds of saplings is impracticable. Nevertheless, two lines of evidence indicate that these GSF values are good estimates of long-term PAR data.

Previously (Rich *et al.*, 1993) we took monthly canopy photographs and monitored PAR continuously for 1 yr, at seven sites along an old growth forest transect at La Selva running through understory and a medium-sized gap. The coefficient of determination (r^2) between the observed PAR and that predicted from the photographs was high (0.72–0.82, 4 different models of analysis).

We also have week-long records of integrated

PAR for four of the species studied here ($N = 10$ saplings/species; Oberbauer *et al.* 1988, 1989). The week-long PAR records clearly are insufficient to represent a yearly cycle. Nevertheless, because the data were taken over many months, they represent a good sample of light environments for these species over the range of understory sites. The median percentage of full sun PAR for each species' saplings corresponded closely to the median GSF values obtained in this study (Table 4). Both of these lines of evidence indicate the GSF values obtained using our analysis protocols and the program CANOPY correspond closely to actual percentage of full sun PAR at the saplings' microsites.

Our second measure of crown lighting, crown position index, has the great advantage of being rapidly and easily applicable to trees of any size under virtually any field conditions. A disadvantage of this method is that a great deal of the information for understory saplings is contained in the distinctions among high, medium, and low lateral light categories. These subjective (although highly repeatable, Clark & Clark 1992) distinctions are based on the average structure of the La Selva forest, and may not be directly applicable to other tropical wet forests. Crown position categories are also not readily transformable into physiologically interpretable units, and there are no permanent records that can be reanalyzed later.

Our results show that crown light environment measures are not necessarily correlated with overhead forest structure. *Pithecellobium* saplings, for example, initially were strongly concentrated in gap/building microsites, indicating a correlation between establishment and forest disturbance. The crown light environments of this species' small saplings, however, were not different from those of the group A and B species, which were found primarily under mature phase forest. Although the crown light environment data revealed several ecologically interpretable patterns among the nine species, additional information about regeneration was obtained by simultaneously evaluating the structure of the forest above saplings.

Our measure of forest structure and disturbance history (forest phase) is based on the maximum height of vegetation over a microsite, and has only three categories (gap, building, mature). This simple classification is clearly insufficient to describe the range of understory microhabitats and their disturbance history. For example, sites at the edges of gaps *sensu* Brokaw (1982) but under canopy-level trees would be classified as "mature phase" with our categories, even though such sites generally re-

TABLE 4. Comparison of global site factors obtained by canopy photography in this study and quantum sensor evaluations of PAR for similar sized saplings of the same species at La Selva. PAR was measured with 15–16 sensors per crown at 5-sec intervals for 7 day periods (data from Oberbauer *et al.* 1988, 1989).

Species	Median GSF from photos (N)	Median % full sun PAR (N)
<i>Lecythis</i>	1.6 (70)	1.1 (10)
<i>Minquartia</i>	1.6 (73)	1.7 (10)
<i>Dipteryx</i>	1.6 (73)	1.5 (10)
<i>Pithecellobium</i>	2.2 (43)	1.5 (10)

ceive considerably more light than sites under mature-phase forest not adjacent to gaps (*cf.* Popma *et al.* 1988). In spite of these limitations, forest phase index is easy to apply to trees of any stature, is highly repeatable between trained observers (Clark & Clark 1992), and provides considerable information about disturbance history around an individual.

MANY WAYS TO BE A TROPICAL TREE?—The regeneration patterns of these nine tropical rain forest tree species are clearly differentially linked to disturbance, light, and the relation between the two. A comprehensive understanding of tree regeneration in these forests will require simultaneous measurement of environmental variables and forest structure for all size classes from seed to adult, as well as repeated measurements on the same individuals over a period of at least several years. In addition to species' relations to light and forest structure, there are also interspecific differences in phenology, seed dispersal, morphology, allocation patterns, and physiology (including responses to soil, topography, and pathogens). To deal with these complexities, one possibility is that most tropical rain forest trees are "generalist species within a few major life history guilds" (Hubbell & Foster 1986). Considering the diversity of factors that have been shown to affect tree regeneration, however, we think it is possible that there are many ecologically distinct tree regeneration patterns. The number of such patterns may approach a substantial fraction of the very high number of sympatric tree species common in these forests. To fully answer the question "Why are there so many species of tropical trees?" comparative studies integrating ecological and physiological approaches will ultimately be necessary.

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