

## LIGHT GRADIENT PARTITIONING AMONG TROPICAL TREE SPECIES THROUGH DIFFERENTIAL SEEDLING MORTALITY AND GROWTH

RICHARD K. KOBE

Michigan State University, Department of Forestry, Natural Resources Building,  
East Lansing, Michigan 48824-1222 USA

**Abstract.** To characterize species differences in light-dependent mortality and growth, I transplanted seedlings of four related tree species into a range of light environments (<1% to 85% full sun) on alluvial soils at La Selva Biological Station, Costa Rica. With maximum likelihood techniques, I fit species-specific, nonlinear regression models of seedling probability of mortality and radial growth as functions of light availability for *Trophis racemosa*, *Castilla elastica*, *Pourouma aspera*, and *Cecropia obtusifolia* (Family Moraceae, latter two also classified as Cecropiaceae).

Models characterizing mortality in the first year of seedling life showed significant differences among the species, both in functional forms and in model parameter estimates. All species decreased in mortality with increases in light to 20% full sun. Above 20% full sun, the mortality of *T. racemosa* and *Castilla elastica* continued to decrease, while that of *Cecropia obtusifolia* remained constant and that of *P. aspera* increased. At <10% full sun, there was a fivefold difference in mortality probability; *T. racemosa* had the highest survivorship, followed by *C. elastica*, *P. aspera*, and *C. obtusifolia*. Mortality models for the initial 4 mo of the experiment revealed significant size effects for all species except *P. aspera* and increased mortality under high light for *P. aspera* and *T. racemosa*.

In contrast, radial growth of all species increased with light availability. The radial growth models, based upon only variation in light availability and tree size, accounted for 60–86% of the variation in growth. *Cecropia obtusifolia* occupied the lowest rank in radial growth at <50% full sun and the highest radial growth at light levels >75% full sun.

When considered together, the mortality and growth models revealed that differences in species performance could lead to light gradient partitioning. At distinct light levels, each species showed the highest growth relative to other surviving species. Neither growth nor mortality considered alone revealed this specialization. Light gradient partitioning provides an explanation for successional dynamics and suggests that tropical tree species coexistence and diversity is at least partly maintained through niche differentiation.

**Key words:** forest dynamics; forest succession; gap partitioning; growth; mortality; nonequilibrium forest dynamics; seedling; shade tolerance; species coexistence; survivorship; tropical forests; tropical tree diversity.

### INTRODUCTION

For temperate and tropical trees, surviving and growing through juvenile stages are major bottlenecks to achieving canopy occupancy. Thus it is not surprising that tree species differences in juvenile growth and survivorship strongly influence forest dynamics, succession, and species composition and diversity (Good and Good 1972, Clark and Clark 1992, Pacala et al. 1996, Kobe and Coates 1997).

In the tropics, studies of juvenile tree performance in relation to resource availability have provided conflicting results. In general, shadehouse studies have shown species differences in growth (Popma and Bongers 1988, Kitajima 1994) and low-light survivorship (Augsburger 1984, Kitajima 1994). But results of field studies are more ambiguous. Species differences in light-dependent growth and survival have been shown

for saplings at La Selva, Costa Rica (Clark and Clark 1992) and for transplanted seedlings in Sri Lanka (Ash-ton et al. 1995). In contrast, tree species appeared to be randomly distributed with respect to canopy openness on a permanent plot at La Selva (Lieberman et al. 1995), and few species responded to presumed variation in light availability on the 50-ha plot at Barro Colorado Island (BCI), Panama (Welden et al. 1991).

These conflicting results might be partly attributed to variation in tree size among the different studies. Welden et al. (1991) examined trees  $\geq 1$  cm diameter at breast height (dbh), Lieberman et al. (1995) included trees  $\geq 10$  cm dbh, and Clark and Clark (1992) examined saplings  $\geq 50$  cm height to mature trees  $\geq 70$  cm dbh. This degree of size variation among studies could have substantial influence on whether species differences are detected (Condit et al. 1995).

Another reason for conflicting results is that gaps and light availability have been characterized with various subjective indices and definitions, a source of

Manuscript received 25 November 1996; revised 2 February 1998; accepted 26 February 1998.

much debate in tropical (and temperate) forest ecology (Brokaw 1982, Popma et al. 1988, van der Meer et al. 1994). But it is not tree-fall gaps per se, but rather the spatial heterogeneity in resources they cause that affect juvenile tree performance and community dynamics. Rather than direct measurements of light intensity, most studies have substituted surrogates such as “low and high canopies” (Welden et al. 1991), “crown illumination indices” (Clark and Clark 1992), and indices of canopy closure based on heights and distances of neighboring trees (Lieberman et al. 1995). A more mechanistic understanding of tropical forest dynamics requires more direct measurements of resource availability and species performance responses to those resources.

Resolution of species differences in mortality also has been limited by a lack of analytical techniques to relate mortality to microenvironments. Mortality rates are often reported on a forest-wide basis (see Condit et al. 1995), ignoring species differences. The few studies reporting species-specific mortality rates usually fail to account for the influence of resources on mortality (e.g., Primack et al. 1985, Alvarez-Buylla and Martinez-Ramos 1992). Mortality rates without information on resource availability yield limited insight into species life histories.

In this paper, I examine intra- and interspecific variation among tropical tree juveniles with nonlinear regression models of mortality and growth as functions of light availability and plant size. The models characterize the “average” juvenile of a species and were calibrated with maximum likelihood techniques from seedlings that were transplanted into a range of field light environments at La Selva Biological Station, Costa Rica. Hemispherical canopy photos were used to calculate light availability. My objectives in developing these models were to: (1) test for species-specific differences in the functional relationships between light availability and growth and mortality; (2) predict what species dominates in given light environments; and (3) evaluate model predictions with respect to species partitioning of light gradients.

## METHODS

### *Species and sites*

I conducted this study at the Organization for Tropical Studies' La Selva Biological Station (10°26' N, 83°59' W), Puerto Viejo de Sarapiquí, Costa Rica (McDade and Hartshorn 1994).

From <1% to 85% full sun, I transplanted seedlings of four related tree species, classified in family Moraceae (Croat 1978) or sister families Moraceae and Cecropiaceae (Hammell 1986a, b). Mature individuals of the species co-occur in secondary forests, but are associated with different successional stages as seedlings and saplings. *Cecropia obtusifolia* juveniles are rarely encountered in the understory (Croat 1978, Ham-

mell 1986a, Clark and Clark 1992), while *Castilla elastica* can occur in secondary forest understory (Hammell 1986b). Juveniles of *Trophis racemosa* and *Pourouma aspera* can be found in primary and secondary forest understories (Croat 1978, Hammell 1986b). Henceforth, these species will be referred to by genus name only.

All transplant plots were located on the same alluvial soil type in the edge buffer zones of a large experiment on productivity and nutrient conservation in artificial plant communities (Huertos Project: Haggard and Ewel 1994) and in nearby secondary forest and abandoned cacao plantations. The study area is a flat alluvial floodplain situated on a peninsula formed by the confluence of the Puerto Viejo and Sarapiquí rivers. The soil is well drained to excessively well drained and has been classified as a mixed isohyperthermic, possibly andic, fluventic Dystropept (Haggard and Ewel 1994). The A horizon extends to ~15 cm depth. All soil horizons contain relatively high concentrations of essential elements (Haggard and Ewel 1994).

### *Field methods and experimental design*

To include genetic variation, seedlings were collected from vicinities of at least three nonadjacent parent trees. In contrast, many studies have collected seeds or seedlings from one parent (e.g., Popma and Bongers 1988, Strauss-Debenedetti and Bazzaz 1991, Kitajima 1994).

I transplanted seedlings into four coarse groupings of light availability (understory, small gap, large gap, and open). Variation between and within groupings resulted in nearly continuous light availability from 0 to 85% full sun, but with sparse coverage between 15 and 35%. The abandoned cacao plantation and secondary forests were used for understory and small gap groupings. Aside from minimal removal of low branches and understory vegetation, no trees were cut to manipulate light levels. Light environments representative of large gap and open areas were attained in the Huertos project buffer zones, the placement of which was guided by a map of light isoclines of direct beam radiation developed for this site (Galo et al. 1992). Four months after transplanting, light availability was quantified for each seedling with a hemispherical canopy photograph used to calculate Canham's (1988) Gap Light Index (GLI).

I established 10 plots in each of the four light groupings. In each of the total 40 plots, I transplanted four individuals of each of the four species to randomly assigned positions (i.e., 16 individuals per plot). Thus the experiment was initiated with a total of 640 seedlings (i.e., four species  $\times$  four light groupings  $\times$  10 plots  $\times$  four individuals/species/plot).

To isolate light availability as an independent variable, I minimized intraplot root competition through seedling spacing and weed removal; trenching the plot periphery to 25 cm depth minimized root intrusion from plants outside the plot. Understory and small gap

TABLE 1. Initial height of seedlings, maximum likelihood parameter estimates, and bootstrapped 95% support interval (in italics) for the "best fit" mortality model for  $T_1$ . "Best fit" models include all significant parameters ( $P \leq 0.05$ ), determined through likelihood ratio tests.

Species	Mean initial height (cm) <sup>†</sup>	Best model	A	B	Threshold <sup>‡</sup>	C <sup>‡</sup>	$\phi$ <sup>‡</sup>
<i>Pourouma</i>	6.16 (2.4–11.3)	IV	0.372 (0.237–0.575)	0.137 (0.018–0.348)	14.368 (3.794–33.352)	0.0343 (0.143–0.0522)	...
<i>Trophis</i>	11.76 (4.3–24.2)	IV	0.278 (0.066–0.931)	0.0885 (0.0022–0.3923)	19.895 (4.341–75.820)	0.055 (0.014–0.424)	0.159 (0.066–0.254)
<i>Castilla</i>	14.65 (5.4–26.9)	I	0.245 (0.036–0.898)	0.011 (0.0–0.0321)	...	...	0.134 (0.0204–0.239)
<i>Cecropia</i>	3.92 (1.0–15.1)	I	1.000 (0.510–2.569)	0.0421 (0.0316–0.0563)	...	...	0.133 (0.002–0.321)

<sup>†</sup> The range is reported in parentheses.

<sup>‡</sup> Ellipses (...) denote that the parameter estimate was not significantly different from null in tests of models that included the parameter (see Fig. 2).

plots were  $2 \times 2$  m with minimum spacing of 0.5 m between seedlings. The large gap and open environment plots were  $3 \times 3$  m with minimum spacing of 0.75 m between seedlings. Seedling death and harvesting during the experiment increased distance between living seedlings. Weeds within plots were cut with a machete approximately every 2 mo. Leaf litter was removed when necessary to avoid burial of seedlings.

Because of phenological variation in seedling production, the transplanted *Trophis* and *Castilla* seedlings were larger and 1–7 mo older than *Cecropia* and *Pourouma* seedlings at  $T_0$  (see Table 1). In late March 1993, I collected newly emerged *Trophis* and *Castilla* seedlings and planted them in plastic nursery bags under shade cloth (to minimize growth) until transplanting. *Cecropia* and *Pourouma* seedlings, unavailable in March, were collected from the field in November and immediately transplanted to the plots.

I transplanted seedlings into plots in November and December 1993, during the transition from rainy to dry seasons. Six continuous days of rain after planting minimized transplant shock. To guard further against transplanting artifacts, seedlings in poor condition were replaced until the initial measurement (on 13 December 1993), designated as the start of the experiment ( $T_0$ ). I assessed mortality and growth on ~15 April 1994 ( $T_1$ ), 21 October 1994 ( $T_2$ ), and 11 February 1995 ( $T_3$ ). Census interval lengths are 4 ( $T_{0-1}$ ), 6.25 ( $T_{1-2}$ ), and 3.75 mo ( $T_{2-3}$ ). Calipers were used to measure (to the nearest 0.1 mm) stem diameter at ground level or at the top of the root collar if it emerged aboveground. Stem diameter was not measured at  $T_0$  because the soft stem tissue of the seedlings may have led to measurement error.

#### Mortality likelihood function

The goal of this analysis was to characterize an individual seedling's probability of mortality as a function of light availability. I used survival analysis and maximum likelihood methods to parameterize mortal-

ity models; likelihood ratio tests (LRTs) (Edwards 1992) and Akaike's information criteria (AIC) (Sakamoto et al. 1986) were used to compare four functional forms. Before describing the models that were evaluated, I first explain the likelihood function that provides the statistical basis for comparing functional forms and estimating parameters.

Survivorship is a binomial random variable with likelihood function:

$$L = \binom{N}{D} [F(T)]^D [1 - F(T)]^{(N-D)} \quad (1)$$

where  $N$  is the number of seedlings starting the experiment,  $D$  is the number of seedlings dying, and  $F(T)$  is the probability of mortality during time interval  $T$ . As the goal was to characterize mortality as a function of light,  $F(T)$  was specified as a function of light availability. The constant  $\binom{N}{D}$  does not affect fits and thus is hereafter omitted.

Eq. 1 must account for the three census intervals of the seedling transplant study; thus the distribution of lifetimes  $F(T)$  has three bins,  $T_{0-1}$ ,  $T_{1-2}$ , and  $T_{2-3}$ , with durations of 4, 6.25, and 3.75 mo, respectively. Let  $F(T_{j-1,j})$  be the probability of dying on interval  $(j - 1, j)$ . Assuming that the rate of mortality is constant,  $F(T_{j-1,j})$  can be specified with an exponential density

$$\begin{aligned} F(T_{j-1,j}) &= \int_{j-1}^j M(\text{light}; \beta) \exp[-M(\text{light}; \beta)t] dt \\ &= \exp[-M(\text{light}; \beta)(j - 1)] \\ &\quad - \exp[-M(\text{light}; \beta)j] \end{aligned} \quad (2)$$

where  $M(\text{light}; \beta)$  is a function composed of light as an explanatory variable and set of parameters  $\beta$ .

If an individual is censored (survives until the end of the experiment or is harvested), then its contribution to the likelihood is  $S(T_j)$  where  $T_j$  is the time of censoring (Cox and Oakes 1984).  $S(T_j)$  specifies the probability of survival beyond censoring time  $T_j$ :

$$S(T_j) = 1 - F(T_j). \quad (3)$$

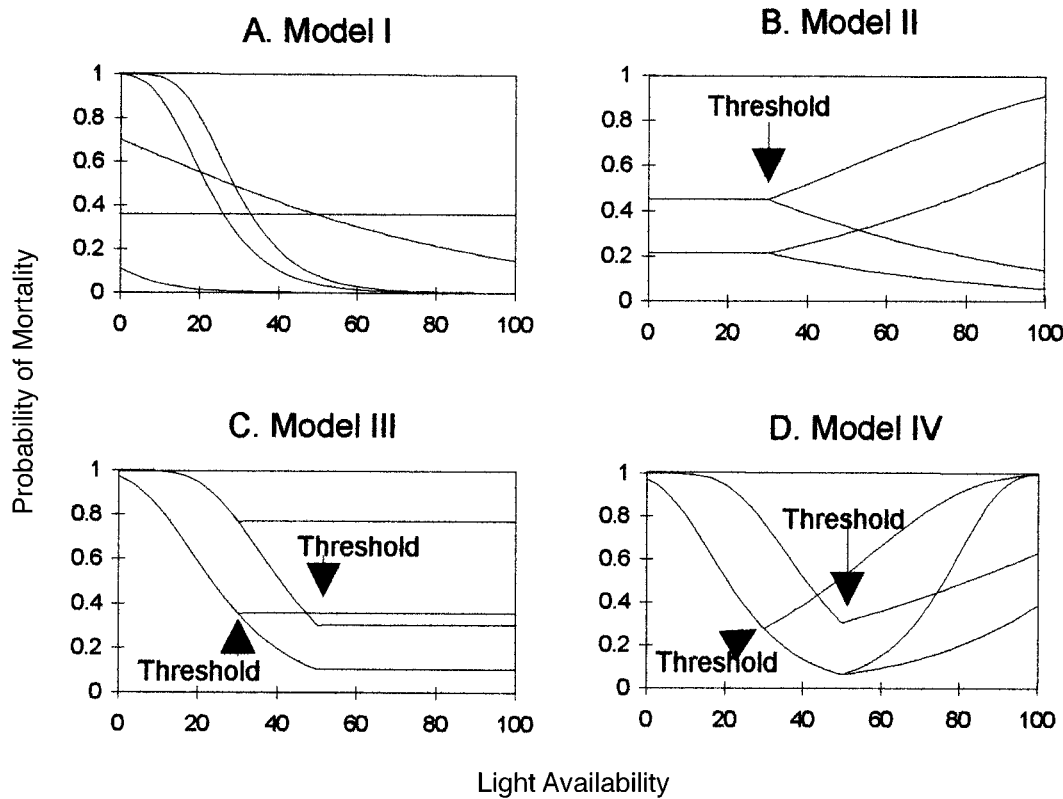


FIG. 1. Curves generated from the four mortality models,  $[M(\text{light}; \beta)]$ . Examples show annual probability of mortality, that is,  $F(T_{0,12}) = 1 - \exp[-M(\text{light}; \beta) \times 12]$ . (A) Model I: decay in mortality with increases in light availability. (B) Model II: constant probability of mortality below a threshold and increases or decreases in mortality above the threshold. (C) Model III: mortality decreases to a threshold and is constant above the threshold. (D) Model IV: mortality decreases to a threshold and increases above the threshold.

Thus the likelihood function for this data set is

$$L = \prod_{i=1}^D F_i[T_{j-1,j} | M(\text{light}; \beta)] \prod_{i=1}^{N-D} S_i[T_j | M(\text{light}; \beta)]. \quad (4)$$

#### Mortality model formulations

The functional forms that I tested for  $M(\text{light}; \beta)$  provide mathematical characterizations of the wide range of mortality responses that I observed in the field (Fig. 1). Different functional forms can be viewed as competing hypotheses of the functional relationship between light availability and probability of mortality (see *Model comparisons* below). The following four models were evaluated for  $M(\text{light}; \beta)$ .

**Model I: Mortality risk decreases as light availability increases.**—This behavior can be characterized with a simple two-parameter negative exponential function (Fig. 1A):

$$M(\text{light}; \beta) = A \exp(-B \times \text{light}) \quad (5)$$

$0 < A < \infty$ ,  $B \geq 0$ . The parameters  $A$  and  $B$  were estimated for each species. As  $A$  increases, mortality at zero light increases.  $B$  represents the sensitivity of

survivorship to changes in light availability. Eq. 5 has been used previously to model mortality as a function of recent growth over a fixed time interval (Kobe et al. 1995, Kobe 1996).

Eq. 5 assumes mortality to be a monotonically decreasing function of light and is inadequate to characterize threshold mortality responses as I observed for *Pourouma* (see *Results*). To address this shortcoming, I derived the following three models where mortality exhibits different sensitivities to light availability above and below an estimated threshold light level.

**Model II. Probability of mortality is constant below a light threshold and can increase or decrease above the threshold (Fig. 1B).**—This can be written as a three-parameter model:

$$M(\text{light}; \beta) = A \quad \text{for light} \leq \text{threshold} \quad (6a)$$

$$M(\text{light}; \beta) = A \exp[-B(\text{light} - \text{threshold})] \quad \text{for light} > \text{threshold}. \quad (6b)$$

Here,  $0 < A < \infty$ ,  $-\infty < B < \infty$ .  $A$ ,  $B$ , and threshold are species-specific parameters.

**Model III. Probability of mortality decreases to a**



light threshold and is constant above the threshold (Fig. 1C).—This can be written as

$$M(\text{light}; \beta) = A \exp(-B \times \text{light})$$

for light  $\leq$  threshold (7a)

$$M(\text{light}; \beta) = A \exp(-B \times \text{threshold})$$

for light  $>$  threshold. (7b)

Here,  $0 < A < \infty$ ,  $B \geq 0$ .  $A$ ,  $B$ , and Threshold are species-specific parameters.

*Model IV. Mortality decreases to a threshold of light intensity; above the threshold, mortality can change in magnitude and direction (Fig. 1D).*—This behavior can be characterized as a four parameter model:

$$M(\text{light}; \beta) = A \exp(-B \times \text{light})$$

for light  $\leq$  threshold (8a)

$$M(\text{light}; \beta) = A \exp[-B \times \text{threshold} + C * (\text{light} - \text{threshold})]$$

for light  $>$  threshold. (8b)

Here,  $0 < A < \infty$ ,  $B \geq 0$ ,  $C \geq 0$ .  $A$ ,  $B$ ,  $C$ , and threshold are species-specific parameters.

#### Mortality model parameterizations and comparisons

I developed models to characterize approximately the first year of seedling mortality. To minimize potential nursery carryover effects, I discarded  $T_{0-1}$  census data for *Trophis* and *Castilla* in calibrating “first-year” mortality models;  $A$  and  $B$  parameter estimates based on  $T_{1-2}$  and  $T_{2-3}$  (10 mo of data) vs. all three census intervals were statistically indistinguishable (asymptotic 95% support, figure not shown). *Cecropia* and *Pourouma* first-year models were calibrated from data from all three census intervals (14 mo of data), because these species had been transplanted directly from other field locations. In addition to the “first-year” models, I also developed mortality models based only on the first time interval ( $T_{0-1}$ ).

For each species, sets of parameters  $\beta$  were estimated for the four functional forms of  $M(\text{light}; \beta)$  by maximizing the likelihood of Eq. 4 on  $\beta$  the parameter space was searched with the Metropolis algorithm (Szymura and Barton 1986). Support bands (95%) were developed with two methods. In a bootstrapping procedure, 1000 data sets for each species were created by resampling with replacement, and parameters  $\beta$  were estimated for each data set. Each  $\beta$  was used to predict mortality at specified light levels, and the 25th and 975th ranked predictions yielded bootstrapped 95% support bands. In the second method, the likelihood ratio test was inverted to construct the asymptotic 95% support regions for parameters  $\beta$ , which were then propagated through the models. The two methods yielded similar support bands and only bootstrapped bands are reported here. All statistical analyses were

performed with programs that I have written in Turbo Pascal.

Models were compared with Likelihood Ratio Tests (nested models) and Akaike's Information Criteria (nonnested models). Fig. 2 shows the relationships among models, how they are nested, and LRTs. For example, the fit of Model IV (a four-parameter model) vs. Model III (a three-parameter model) was tested with an LRT of parameter  $C = 0$  vs.  $C$  fitted to the data (Fig. 2). All nested models were compared in this way at a significance level of 0.05 (IV vs. III, III vs. I, IV vs. II, II vs. I, and IV vs. I) (Fig. 2). Models II and III were not nested and therefore were compared with AIC. To test for the significance of light availability, all models were compared to a null model of no light effect (LRTs of  $B = 0$  and/or  $C = 0$  vs.  $B$  and/or  $C$  fitted to the data).

I also tested for effects of initial seedling size on mortality by adding the term  $(\phi \times \text{height})$  to the exponent of each model. For example,  $(-B \times \text{light})$  in Model I became  $(-B \times \text{light} + \phi \times \text{height})$ . Significance of size was tested with an LRT of parameter  $\phi = 0$  vs.  $\phi$  fitted to the data.

#### Growth

For each species, I estimated a “first-year” radial growth model based on two census intervals ( $T_{1-2}$  and  $T_{2-3}$ ). The models specify radial growth for the average individual of a particular size at a given light level. The growth model is derived from

$$(\text{Radius})_T = (\text{Radius})_0[1 + G(L)]^T + \varepsilon \quad (9)$$

where  $(\text{Radius})_T$  is the radius of an individual seedling at time  $T$  (in months),  $G(L)$  is growth rate as a function of light availability for the average seedling, and the error distribution  $\varepsilon$  is  $N(0, \sigma_\varepsilon)$ , because residuals were normally distributed. Thus, growth over time interval  $T$  is  $(\text{Radius})_T - (\text{Radius})_0 + \varepsilon$ . The likelihood function for the growth data is the product of the probability densities for a normal random variable.

I tested two different functional forms for  $G(L)$ , including a Michaelis-Menten function used by Pacala et al. (1994) to model growth of temperate saplings:

$$G(L) = \frac{P_1 \times L}{\frac{P_1}{P_2} + L} \quad (10)$$

where  $P_1$  and  $P_2$  are species-specific parameters corresponding with asymptotic growth and the slope of the function at zero light, respectively. The second functional form tested for  $G(L)$  was

$$G(L) = \text{Asymp.}[1 - \exp(-S/\text{Asymp.} \times L)] \quad (11)$$

where Asymp. and  $S$  are species-specific estimated parameters and correspond with asymptotic and low-light growth, respectively.

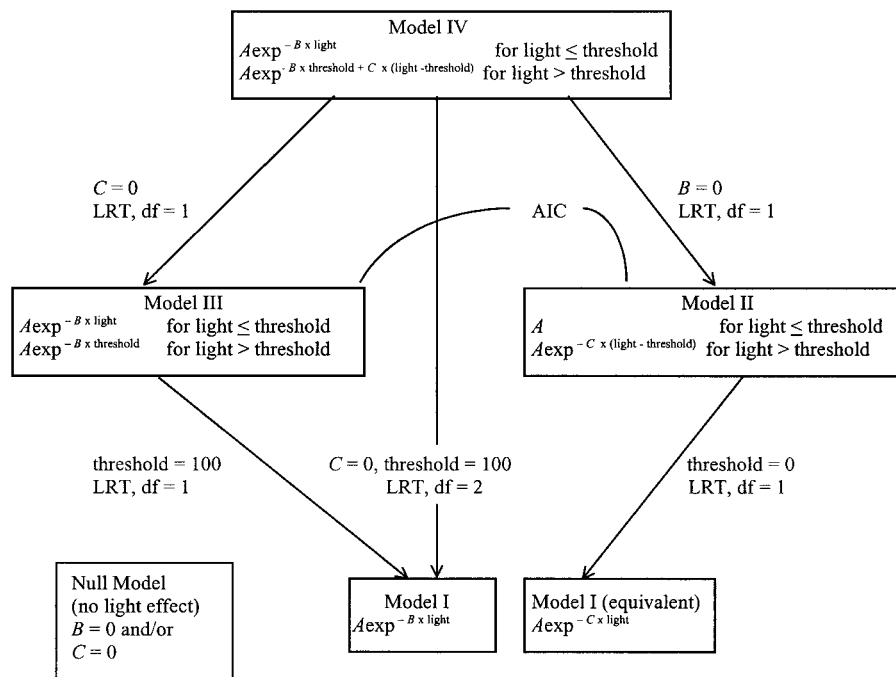


FIG. 2. Diagram of the relationships of the mortality models. All nested models were compared with likelihood ratio tests (LRTs). The basis of LRTs is that a complicated model will simplify to a nested model when a parameter is set to a specific value. Degrees of freedom are as stated. Non-nested models (II and III) were compared with Akaike's Information Criteria.

## RESULTS

### Mortality

**Early seedling mortality ( $T_{0-1}$ ).—**Light-dependent mortality during the first census period fit two models. *Pourouma* and *Trophis* showed decreased mortality with increased light until a threshold of ~15–20% full sun; above this threshold, higher light corresponded with higher mortality (i.e., best fit to model IV, Fig. 2 for LRTs) (Fig. 3 A-B, Table 1). In contrast, the early-successional species, *Castilla* and *Cecropia*, exhibited a decay in mortality with increases in light (model I); threshold models for these species did not provide better fits (LRTs, Fig. 2). *Cecropia* showed the strongest response to light availability (Fig. 3D, Table 1). Light availability was significant for all species (LRTs,  $df = 1-2$ ,  $P \leq 0.05$ ).

Even with my attempt to minimize variation in initial seedling size (Table 1), taller individuals of *Trophis*, *Castilla*, and *Cecropia* were significantly associated with lower mortality at all light levels (Fig. 3B–D) (LRTs,  $df = 1$ ,  $P \leq 0.05$ ). Height was not significant for *Pourouma*, probably the result of having the narrowest range in initial size (Table 1).

Interspecific comparisons of mortality models during  $T_{0-1}$  should be drawn cautiously, because species had different pretransplant histories (see *Methods*). Carryover effects of the nursery and larger initial sizes of *Trophis* and *Castilla* may have resulted in lower mortality. But increased high-light mortality was not likely

due to pretransplant history, because it was exhibited by nursery (*Trophis*) and wild (*Pourouma*) seedlings. Conversely, seedlings with lower mortality in high light were transplanted from the nursery (*Castilla*) and the wild (*Cecropia*).

**First-year mortality models.**—Light availability was significant in the “first-year” mortality models for all species (LRTs,  $df = 1-2$ ,  $P \leq 0.05$ ), but initial seedling height (at  $T_0$ ) was not (LRTs,  $df = 1$ ,  $P > 0.05$ ). At  $<20\%$  full sun, higher light resulted in lower mortality for all species (Fig. 4). Above 20% full sun, however, the species exhibited three responses, necessitating three functional forms to characterize mortality–light relationships (Table 2). *Trophis* and *Castilla* exhibited decreases in mortality (Model I) across a full range of light. Above 21% full sun, *Pourouma* mortality increased (Model IV) and above 19% full sun, *Cecropia* mortality remained constant (Model III, Fig. 4). *Cecropia*'s constant mortality at higher light was probably due to site-specific peccary browsing. Most *Cecropia* individuals dying in high light had been browsed; no unbrowsed *Cecropia* died after  $T_2$ . There was no evidence that browsing contributed to the death of low-light *Cecropia*, but I cannot exclude the possibility that low-light browsing went unobserved. No seedlings of the other species appeared to be browsed. For all species, there was good correspondence between the mortality data and the fitted models (Fig. 5).

Bivariate 95% support regions showed species dif-

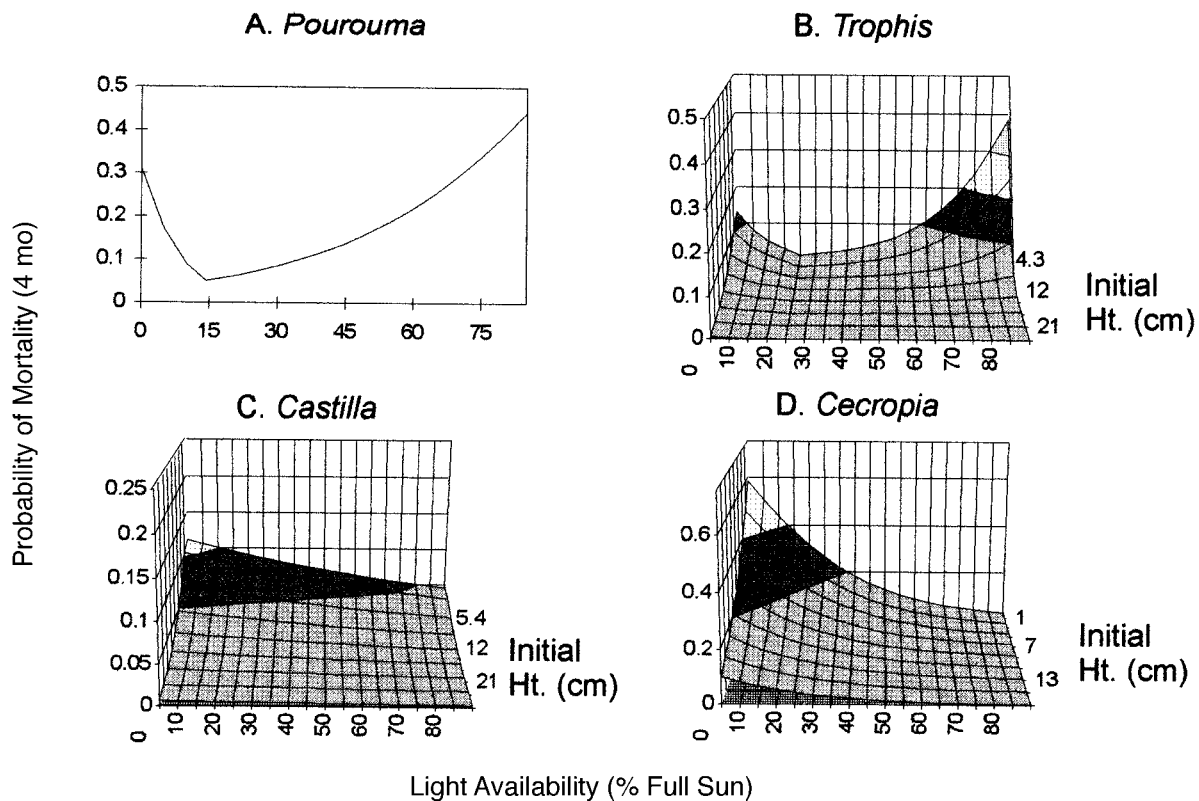


FIG. 3. Seedling mortality models calibrated from the first 4-mo period after transplanting ( $T_{0-1}$ ) for (A) *Pourouma aspera*, (B) *Trophis racemosa*, (C) *Castilla elastica*, and (D) *Cecropia obtusifolia*. Initial seedling size significantly influenced the prediction of mortality in all species except *Pourouma*, and therefore size is not shown as an axis in (A).

ferences in  $A$  and  $B$  estimates of the first-year mortality functions with slight overlap between *Castilla* and *Trophis* (Fig. 6). Even though three models were used to characterize mortality–light relationships for these four species, the  $A$  and  $B$  parameters of the three models specify mortality over  $\sim 0$ – $20\%$  full sun and thus species can be compared directly. This range of light in-

tensity corresponds with understory to large gap gradients (Chazdon and Fetcher 1984).

Support bands (95%) on the relationship between mortality and light also show species differences. At  $<5\%$  full sun, support bands of *Trophis* did not overlap with *Pourouma* or *Cecropia*. At higher light levels ( $>40\%$  full sun), mortality support bands for browsed

FIG. 4. Probability of mortality as a function of light availability standardized to an annual basis, i.e., probability of mortality =  $1 - \exp[-12 \times M(\text{light}; \beta)]$ , with 95% bootstrapped support bands.

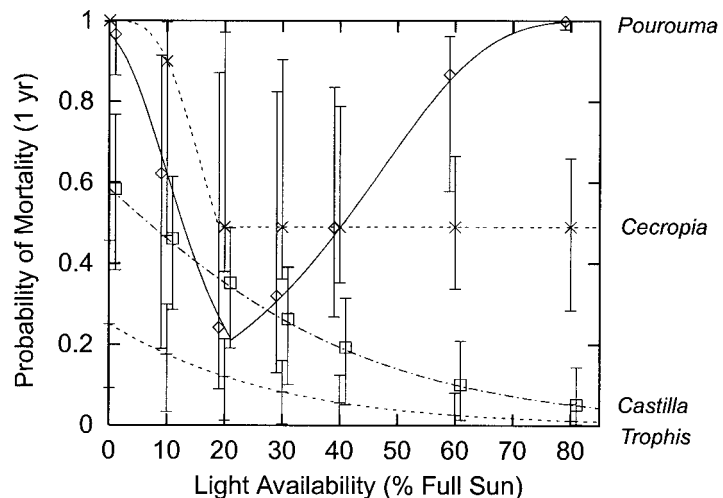


TABLE 2. Maximum likelihood parameter estimates and bootstrapped 95% support interval (in italics) for the “best fit” first-year mortality model. See Table 1 legend for definition of “best fit.”

Species	Best model	A	B	Threshold†	C†
<i>Pouroma</i>	IV	0.2851 <i>(0.1674–0.6518)</i>	0.1257 <i>(0.0116–0.3742)</i>	21.22 <i>(7.20–65.61)</i>	0.0551 <i>(0.029–0.151)</i>
<i>Trophis</i>	I	0.0241 <i>(0.0081–0.0515)</i>	0.0404 <i>(0.0165–0.1468)</i>	...	...
<i>Castilla</i>	I	0.0733 <i>(0.0405–0.1221)</i>	0.0353 <i>(0.0189–0.0712)</i>	...	...
<i>Cecropia</i>	III	0.7520 <i>(0.4975–3.299)</i>	0.1368 <i>(0.0374–0.6656)</i>	18.98 <i>(5.34–76.68)</i>	...

† Ellipses (...) denote that the parameter estimate was not significantly different from null in tests of models that included the parameter (see Fig. 2).

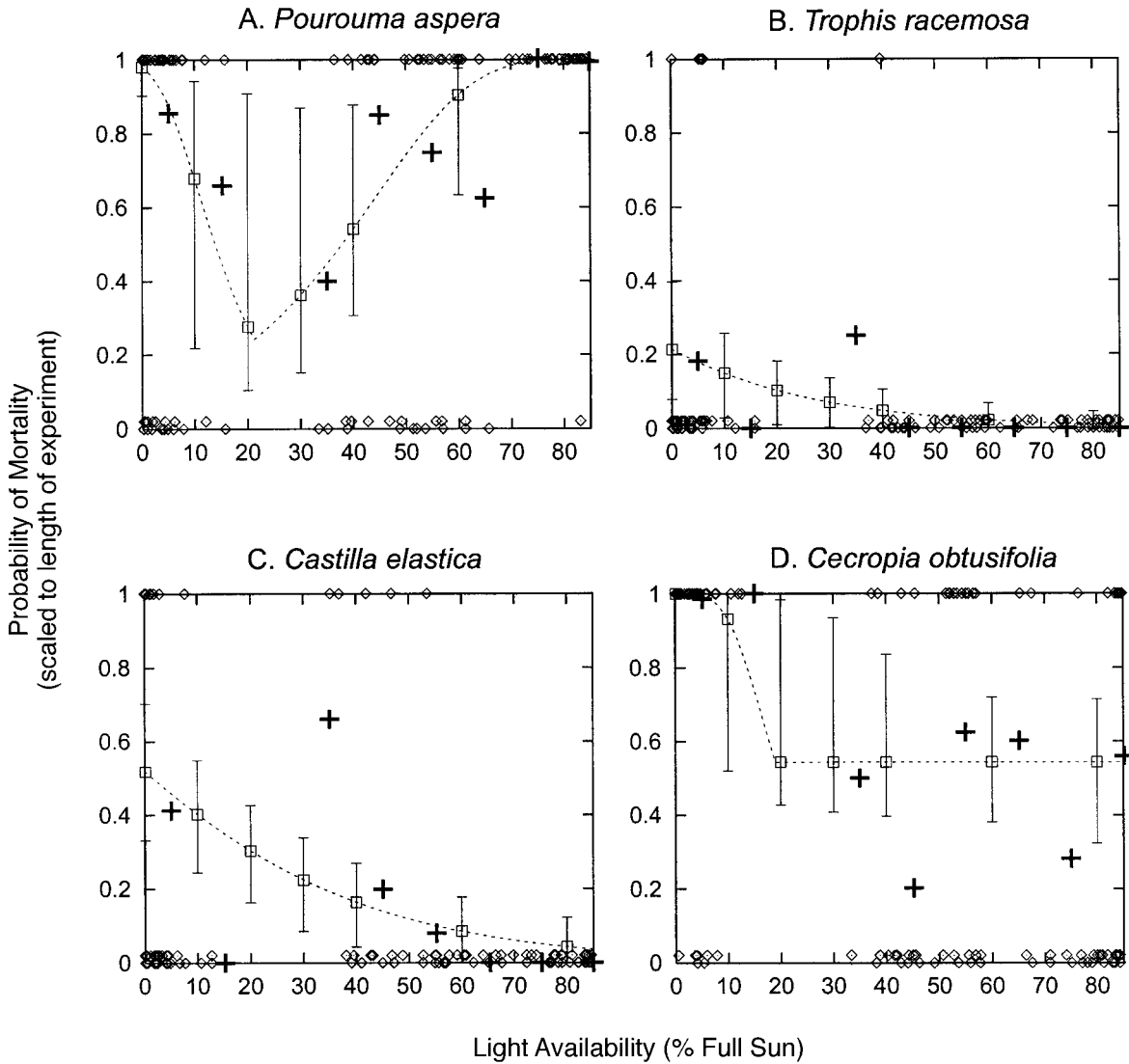


FIG. 5. Fits of mortality functions to raw data and average mortality within 10% light bins (indicated by +). The graph is scaled to the total length of census intervals for each species (see *Methods*). Each  $\diamond$  represents an individual seedling and is plotted along the  $x$ -axis at its measured light level and along the  $y$ -axis according to its fate: dying seedlings are plotted at 1, surviving seedlings are plotted at 0, and harvested seedlings are just above 0.



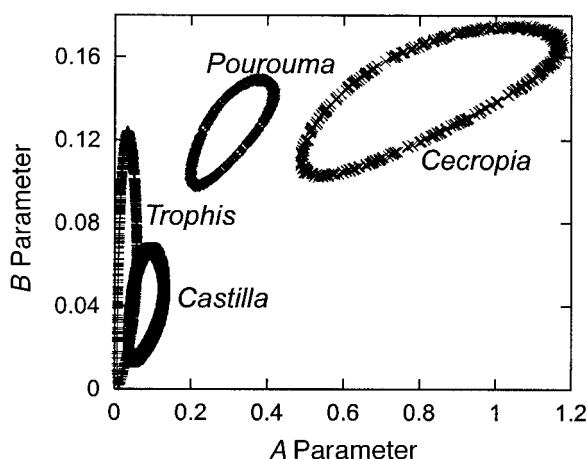


FIG. 6. Asymptotic support regions (95%) of the A and B parameters of the mortality models.

*Cecropia* were higher than *Castilla* and *Trophis*, but unbrowsed *Cecropia* showed similar mortality levels. At >60% light, 95% support for *Pourouma* mortality did not overlap with other species (Fig. 4).

Dead individuals were associated with lower light

levels than lives for all species but *Pourouma* (Fig. 7). However, this analysis wrongly suggested that light did not influence *Pourouma* mortality (compare Figs. 4 and 7) because its hyperbolic response was obscured. For the other species, the lowest light levels at which seedlings survive and the highest levels at which they die provide a measure of shade tolerance consistent with the mortality models: *Trophis* > *Castilla* > *Cecropia*.

Another way of viewing species differences in mortality is to calculate expected lifetimes under different light environments (Fig. 8). If constant mortality rates are assumed, the expected lifetime of a species' seedlings at a specified light level is equivalent to  $1/[M(\text{light}; \beta)]$ . While *Castilla*'s low-light mortality was slightly higher than that of *Trophis* (Fig. 4), the expected low-light (<2% full sun) lifetime for *Castilla* was 1 yr vs. 3.5 yr for *Trophis*. In contrast, the average *Cecropia* seedling under low light would survive for only ~1 mo.

*Trophis* exhibited the highest expected lifetime across all light levels. At light levels <15% full sun, *Castilla* ranked second in expected lifetime. At 15–28% full sun, *Pourouma* ranked second with an expected lifetime >1 yr longer than that of *Castilla*. These

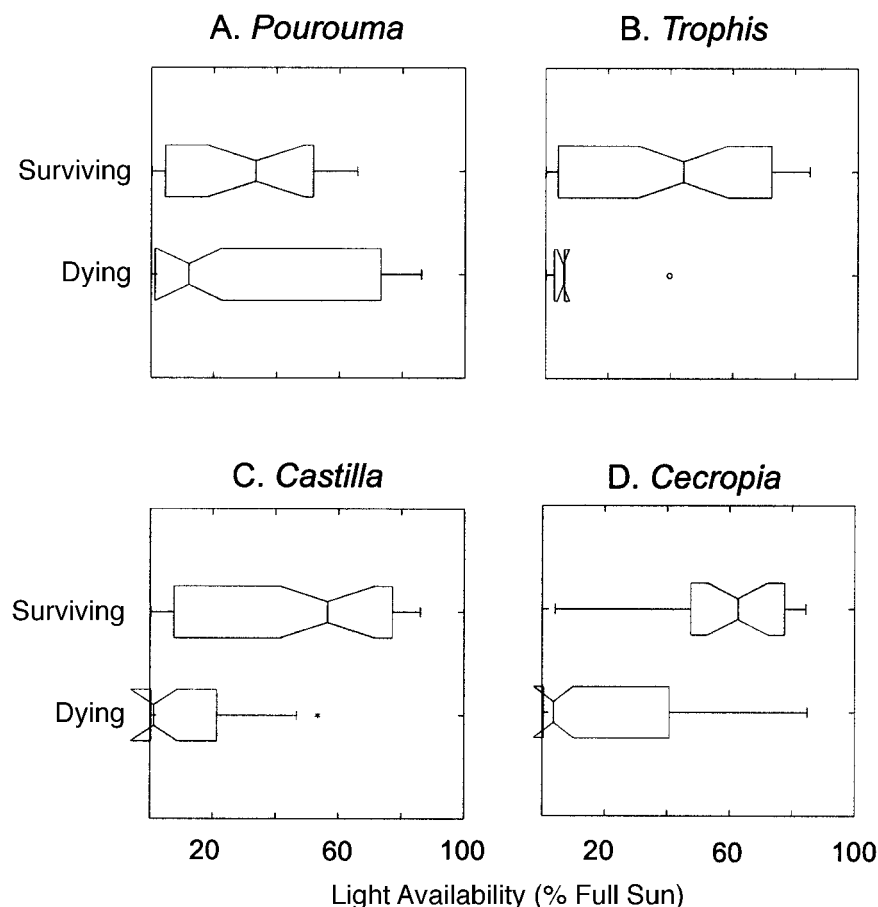


FIG. 7. Distributions of light levels associated with surviving and dying seedlings displayed with notched boxplots.

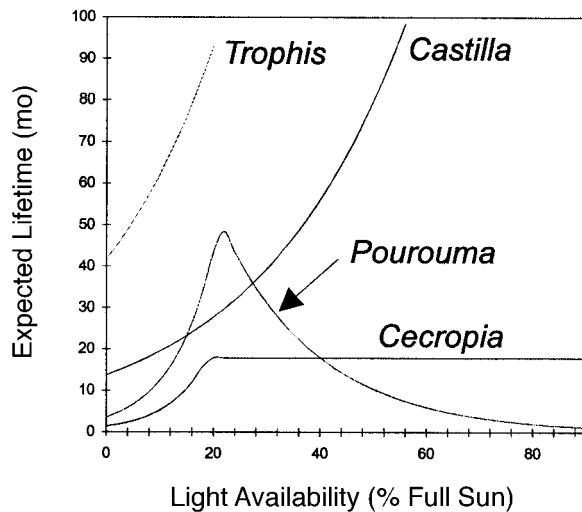


FIG. 8. Expected seedling lifetime as a function of light availability.

results must be viewed conservatively because they sometimes extrapolate beyond the 14-mo length of the study. Furthermore, under higher light availability the juvenile phase could be outgrown before the expected lifetime is reached and the mortality model would no longer apply. For example, *Cecropia*'s expected lifetime at 80% full sun is 20 mo, but, in 12 mo, a 5 mm radius seedling would grow to 55 mm radius.

#### Growth

The Michaelis-Menten function (Eq. 10) for the growth model [ $G(L)$ ] resulted in higher likelihoods for all species than did Eq. 11. Based on the AIC, eq. 10 was used for  $G(L)$ .

In contrast to mortality, all four species showed increases in radial growth with increased light availability (Fig. 9A). The growth residuals plotted as a function of light availability were balanced (plots not shown), supporting the interpretation that high light did not negatively affect radial growth. However, the effects on *Pourouma* growth of light levels >65% full sun are uncertain as no *Pourouma* individuals survived at these levels. These species grew very fast, especially at high-light availability. The fitted models showed that over the course of one year, a standardized 5 mm radius *Cecropia* seedling increased by 14-fold, and the slowest grower at high light, *Trophis*, increased its radius by sixfold (Fig. 9).

The 95% bootstrapped support regions of growth model parameters ( $P_1$  and  $P_2$ ) showed overlap among species (Table 3), except *Cecropia* had a greater high-light growth parameter ( $P_1$ ) and lower low-light parameter ( $P_2$ ) than did *Trophis* and *Castilla*. The 95% support bands on the growth–light relationship also overlapped among species (Fig. 9).

The growth models provided good fits to the data. *Pourouma* showed the poorest fit ( $R^2 = 0.603$ ) (Table

3), while other species had  $R^2$  values  $\geq 0.825$  (Table 3). Residuals also were balanced with respect to actual growth and size (graphs not shown). Model growth predictions (given size and light availability) corresponded well with actual growth (Fig. 10).

#### Species performance trade-offs and light gradient partitioning

To explore the success of seedlings in different light environments, I developed a simple test of species “dominance” using the field-calibrated mortality and growth models. Consider a hypothetical experiment where  $n$  seedlings of each of four species establish at the same time in a given light environment and their fate (i.e., survival and growth) is followed for one year. In order for a species to dominate a light environment, it must have at least one surviving individual and that individual must attain the fastest relative growth among other surviving seedlings. The expectation of the number of individuals surviving at a particular light level is survivorship times  $n$  (i.e., the number of “trials” or seedlings of a species in a light environment).

Fig. 11 shows the results of this hypothetical experiment and reveals light gradient partitioning from 0 to 85% full sun among the four species. *Trophis* was the only species with a surviving individual at <8% full sun ( $n = 2$ ) and therefore was predicted to dominate; it also dominated at 8–12% full sun, because it grew faster than *Castilla*. The highest relative radial growth among survivors gave *Pourouma* dominance at 12–40% full sun, *Castilla* at 40–70% full sun, and *Cecropia* at  $\geq 70\%$  full. With greater abundance of all species ( $n = 5$  and  $n = 10$ ), light gradient partitioning was still evident, but *Pourouma* was expected to have at least one surviving seedling over a wider range of light availability, which resulted in its broader dominance (figure not shown).

#### DISCUSSION

##### Species variation in performance

There was clear variation among these four species in light-dependent growth and mortality. At high light levels, some species differed in radial growth by a factor of two. At low light, probability of mortality varied among species by a factor of five. Interspecific variation in mortality was manifested not only in statistically different parameter estimates, but also in different functional forms. The interspecific variation characterized here is consistent with the results of other studies of tropical (e.g., Clark and Clark 1992, Augspurger 1984, Ashton et al. 1995) and temperate juvenile trees (e.g., Walters et al. 1993, Pacala et al. 1994, Kobe et al. 1995, Kobe and Coates 1997).

Within each species, increases in light availability generally had positive effects on seedling performance, consistent with previous tropical (Fetcher et al. 1983, Popma and Bongers 1988, King 1991, 1994, Kitajima

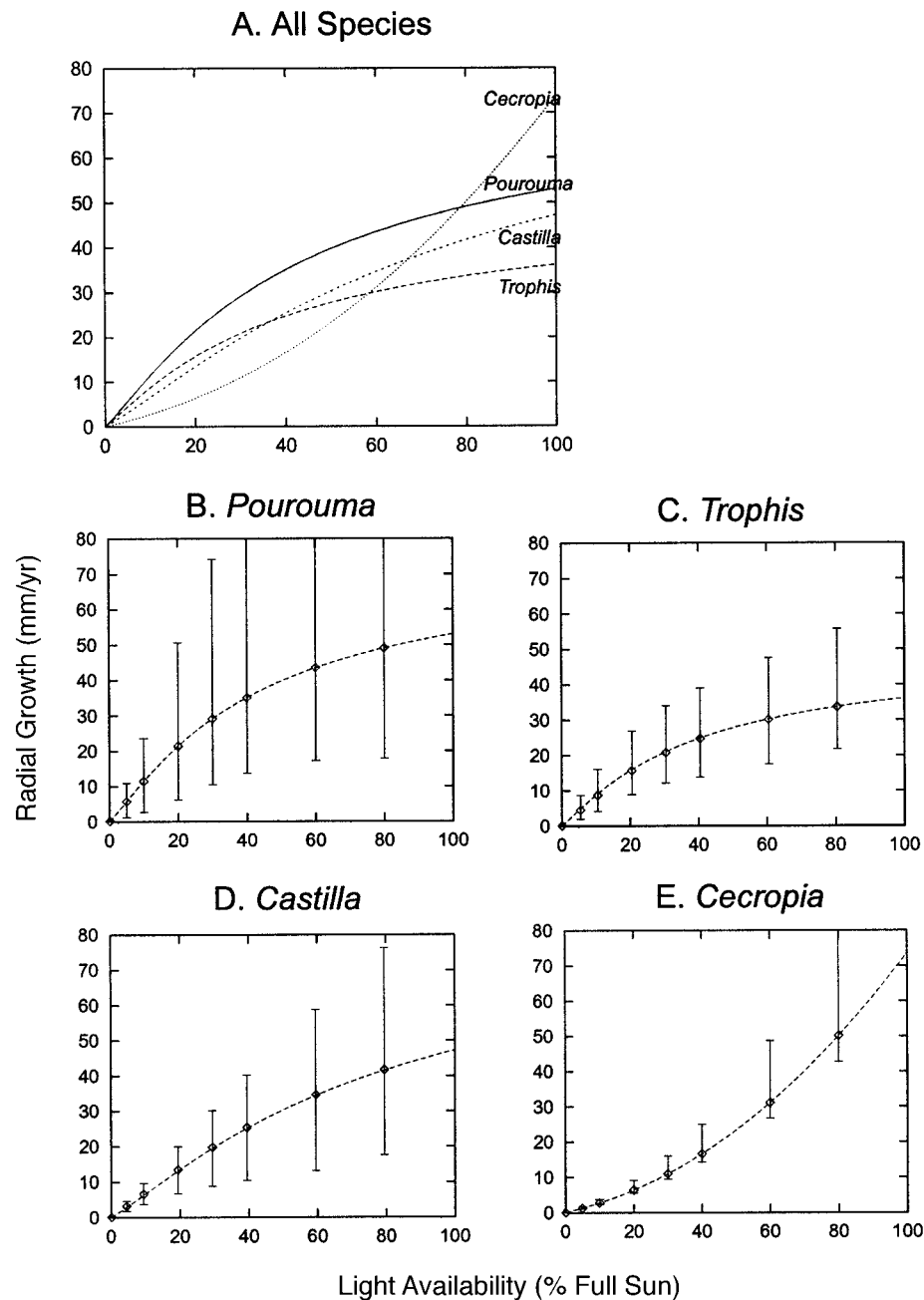


FIG. 9. Fitted models of radial growth as a function of light availability standardized to a 5-mm radius stem. The line represents the mean growth for a species, and the error bars represent the 95% bootstrapped support bands at specified light levels.

1994, Clark and Clark 1992, Ashton et al. 1995) and temperate studies (Walters et al. 1993, Pacala et al. 1994). Seedlings under high light grew from 7 to 14 times faster than their low-light counterparts. Mortality decreased with increases in light availability up to 20% full sun, representative of a light gradient from understory to large gaps (400 m<sup>2</sup>) (Chazdon and Fetcher 1984, Rich et al. 1993).

The inter- and intraspecific variation characterized

by this and other studies contrasts with results that suggest most or all tropical tree species are generalists (Welden et al. 1991, Lieberman et al. 1995). On BCI, Welden et al. (1991) compared sapling ( $\geq 1$  cm dbh) survival and growth between canopy sites categorized as "low" (canopy height <10 m, presumably gaps) and "high" (>10 m, presumably understory). Only 17% of species showed significant survival differences between canopy categories (with lower survival in

TABLE 3. Maximum likelihood parameter estimates, bootstrapped 95% support limits (in italics), and  $R^2$  values for the fitted Michaelis-Menten growth functions to characterize approximately the first year of radial growth.

Species	N	$P_1^\dagger$	$P_2^\dagger$	$R^2$
<i>Pourouma</i>	22	0.2609 ( <i>0.1433–0.9379</i> )	0.0173 ( <i>0.0038–0.0352</i> )	0.603
<i>Trophis</i>	51	0.2211 ( <i>0.1719–0.3483</i> )	0.0145 ( <i>0.0061–0.0278</i> )	0.859
<i>Castilla</i>	53	0.2768 ( <i>0.2231–0.3861</i> )	0.0098 ( <i>0.0056–0.0141</i> )	0.834
<i>Cecropia</i>	1	0.7618 ( <i>0.5990–0.9315</i> )	0.0039 ( <i>0.0035–0.0051</i> )	0.825

Note: The  $R^2$  values are a measure of the fit of the nonlinear growth model to the actual data and are calculated as  $R^2 = 1 - (SS_{\text{resid}}/SS_{\text{total}})$  (Myers 1990).

$^\dagger P_1$  and  $P_2$  are species-specific parameters corresponding with asymptotic growth and the slope of the function at zero, respectively.

high-canopy sites), and 66 of 115 species showed higher growth in low-canopy sites. Welden et al. (1991) acknowledge that true differences between canopy categories could have been obscured by a severe drought,

light heterogeneity within canopy categories, and coarse measurement (to 0.5 cm) of diameter. In a permanent plot of mature forest at La Selva, Lieberman et al. (1995) found that trees  $\geq 10$  cm diameter at breast height (dbh) of most species were randomly distributed in relation to an index of canopy openness. Due to temporal heterogeneity of forest light conditions (Chazdon and Fetcher 1984, Rich et al. 1995), especially over the time scale necessary for a seedling to reach 10 cm dbh, these large trees probably established and grew under light environments very different from those at the time of measurement. Therefore, correlating the static distribution of individuals with present microenvironments is a weak test of species variation (also see Clark and Clark 1992). A more appropriate test is to examine growth and mortality in relation to light availability over a time scale in which light variation is known.

Studies arguing for the functional equivalence of different species (Welden et al. 1991, Lieberman et al. 1995) have focused on larger size classes. Because juvenile tree mortality decreases with increasing size

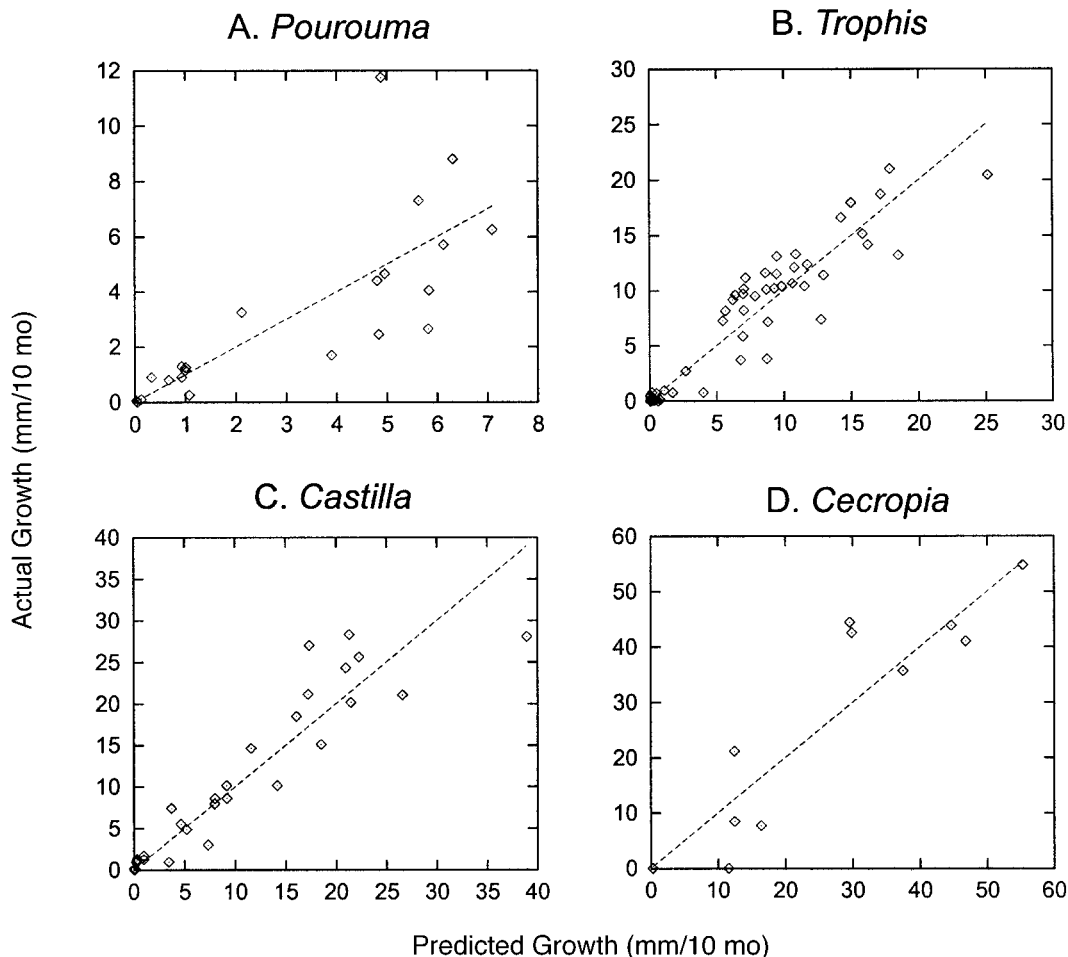
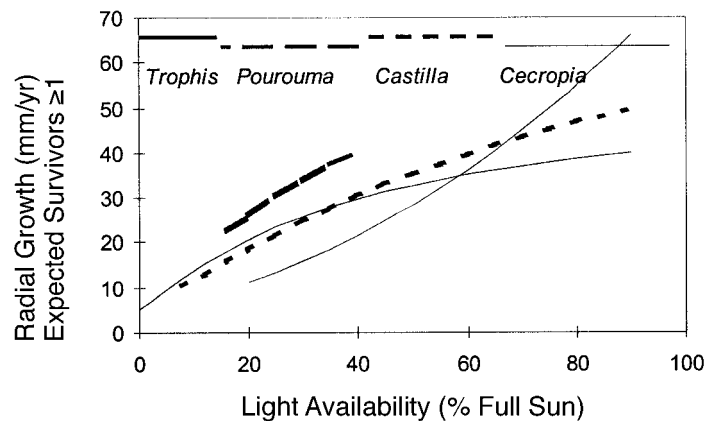


FIG. 10. Actual vs. predicted growth based on light availability and seedling size. The dashed lines in each panel are 1:1.

Fig. 11. Species-specific, annual radial growth of seedlings over the range of light availability where the species is expected to have at least one surviving individual. The lines at the top of each panel represent the range of the light gradient over which the species will have at least one surviving individual and maintain the fastest radial growth (i.e., where the species is expected to be dominant) after 1 yr.



(Clark and Clark 1992, Condit et al. 1995, references in Sheil and May 1996), detection of species differences in mortality becomes more difficult in larger size classes. During the first census, size influenced mortality for all species but *Pourouma*, which had a very narrow range of initial seedling heights. In addition, I found different effects of light availability on mortality in the first 4 mo of seedling life vs. later ages and larger sizes. Similarly, Clark and Clark (1992) found significant differences in crown illumination indices between dying and surviving saplings in nonpioneer species only in size classes <1 cm dbh. On BCI, “colonists” had higher mortality rates than “generalist” species in a size class of 1–9.9 cm dbh, but similar mortality rates in larger size classes (Condit et al. 1995).

This study demonstrates the importance of measuring resource levels directly and examining tree performance over a wide and continuous range of possible resource conditions. Direct quantification of light availability (Canham 1988) provided better resolution to detect species differences than subjective light indices. If I had examined performance at a few predefined conditions (e.g., gaps vs. understory), I would have missed prominent characteristics that distinguish these species, especially the threshold response of *Pourouma* mortality to light.

#### Light gradient partitioning

Among the numerous hypotheses to explain diversity of canopy tree species in the tropics (reviewed in Leigh 1985, Huston 1994), there are two prominent and competing ideas on the relationship between canopy gaps and tree diversity. The “gap partitioning hypothesis” states that variation in resource availability caused by tree-fall gaps contributes to canopy tree diversity by providing opportunities for species to specialize (Ricklefs 1977, Denslow 1980, 1987, Hartshorn 1980, Orians 1982). Alternatively, tropical forest diversity could be maintained by random variation in extinction and migration of functionally equivalent tree species within a few guilds (Hubbell and Foster 1986, Condit et al.

1992). In this view, species composition is largely uninfluenced by tree-fall gaps.

The results of this study show not only that these four species differ in light-dependent growth and survival, but also that these differences could lead to light gradient partitioning (Fig. 11). The potential partitioning shown here does not support the idea that tropical tree species occupy narrow and exclusive niches, a criterion that has been used to test the gap partitioning hypothesis (e.g., Weldin et al. 1991, Lieberman et al. 1995). Rather than exclusive occurrence, this study suggests that partitioning operates through changes in species performance rank; each species survives and attains the highest relative rank in growth over a specific range of light intensities.

While this study is consistent with the idea that species life history variation could contribute to the maintenance of tropical tree diversity, it does not exclude the hypotheses that numerous tropical tree species could be competitive equivalents and that chance plays a role in tropical forest dynamics. The small number of studied species segregated over a broad light gradient, suggesting that they may represent different guilds. Large disturbances would be necessary to create sufficient variation in light to enable coexistence by partitioning for these species. Over endogenous light variation from understory to large 400 m<sup>2</sup> gap (or 0–35% full sun) (Chazdon and Fetcher 1984), the performance-based dominance test provided a potential explanation for the coexistence of only *Trophis* and *Pourouma*.

While Popma and Bongers (1988) have argued that growth is paramount over mortality in determining shade tolerance, this study illustrates that both mortality and growth are critical processes in light-gradient partitioning. *Trophis* was predicted to dominate at low light because of its high survivorship, but at higher light, *Trophis* grew slowly relative to other surviving species and thus was not dominant. Similarly, *Cecropia* dominated only high-light environments, because it grew and survived poorly under lower light. Trade-offs



between high-light growth and low-light survivorship are critical to predicting species coexistence and successional dynamics in temperate forests (Kobe et al. 1995, Pacala et al. 1996) and also could be operating in tropical systems. In addition to this study, evidence of this trade-off for tropical species has been suggested by the results of Hubbell and Foster (1992) and Kitajima (1994).

This study provides support for the necessary preconditions of species coexistence through light-gradient partitioning—interspecific variation in light-dependent mortality and growth that leads to changes in species dominance at different light levels. There is a need for more studies that explicitly characterize tropical seedling and sapling performance over a wide and continuous range of light availability. In future studies, the question “how many life histories of tropical trees are there?” (Swaine and Whitmore 1988, Whitmore 1989, Welden et al. 1991, Clark and Clark 1992) should take into account continuous variation among species and that life history variation is only relevant to coexistence when there are changes in species performance rank across possible resource conditions. The relevant questions then become: What strategic trade-offs (e.g., low-light survivorship vs. high-light growth vs. low-light growth vs. dispersal ability) (sensu Pacala et al. 1996), if any, define variation in species life histories? And does the distribution of tropical tree species along these trade-offs show resource partitioning and provide the necessary prerequisites for species coexistence?

#### ACKNOWLEDGMENTS

This research was initiated as a dissertation chapter at the University of Connecticut and was made possible by grants from the Organization for Tropical Studies (Mellon Ecosystem Research Fund), University of Connecticut Graduate School (extra-ordinary expense award) and Department of Ecology and Evolutionary Biology (NSF Graduate Traineeship in the Evolution, Ecology, and Conservation of Biodiversity—BIR-9256616). The support of La Selva and TRI-ALS project nursery staff are greatly appreciated. I am indebted to Jack Ewel, Seth Bigelow, Jeremy Haggard, Silvino Villegas, and Virgilio Alvarado and the rest of the Huertos Project (supported by NSF DEB 9318403) for access to and maintenance of field plots. Robin Chazdon and the Bosques Project always generously loaned equipment. Bernal Paniagua and Renée Leone helped with data collection. I thank Jim Clark, John Silander, Robin Chazdon, Robert Colwell, Steve Pacala, Charles Canham, Deborah Clark, and two anonymous reviewers for their comments on this manuscript. Orlando Vargas provided help with seedling identifications. Frank Berendse and the Department of Terrestrial Ecology and Nature Conservation at Wageningen Agricultural University, The Netherlands, hosted me while this manuscript was rewritten.

#### LITERATURE CITED

- Alvarez-Buylla, E. R., and M. Martinez-Ramos. 1992. Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree—an evaluation of the climax-pioneer paradigm for tropical rain forests. *Journal of Ecology* **80**: 275–290.
- Ashton, P. M. S., C. V. S. Gunatilleke, and I. A. U. N. Gunatilleke. 1995. Seedling survival and growth of four Shorea species in a Sri Lankan rainforest. *Journal of Tropical Ecology* **11**:263–279.
- Augsburger, C. K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* **72**:777–795.
- Brokaw, N. V. L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* **11**:158–160.
- Canham, C. D. 1988. An index for understory light levels in and around canopy gaps. *Ecology* **69**:1634–1638.
- Chazdon, R. L., and N. Fetcher. 1984. Light environments of tropical forests. Pages 49–57 in E. Medina, H. A. Mooney, and C. Vazquez-Yanes, editors. *Physiological ecology of plants of the wet tropics*. Dr. W. Junk, The Hague, The Netherlands.
- Clark, D. A., and D. B. Clark. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs* **62**:315–344.
- Condit, R., S. P. Hubbell, and R. B. Foster. 1992. Short-term dynamics of a neotropical forest: change within limits. *BioScience* **42**:822–888.
- Condit, R., S. P. Hubbell, and R. B. Foster. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* **65**: 419–439.
- Cox, D. R., and D. Oakes. 1984. *Analysis of survival data*. Chapman and Hall, New York, New York, USA.
- Croat, T. B. 1978. Flora of Barro Colorado Island. Pages 342–362 in *Moraceae*. Stanford University Press, Palo Alto, California, USA.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* **12** (Supplement):47–55.
- . 1987. Tropical forest gaps and tree species diversity. *Annual Review of Ecology and Systematics* **18**:431–451.
- Edwards, A. W. F. 1992. *Likelihood*. Revised edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Fetcher, N., B. R. Strain, and S. F. Oberbauer. 1983. Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. *Oecologia* **58**:314–319.
- Galo, A. T., P. M. Rich, and J. J. Ewel. 1992. Effects of forest edges on the solar radiation regime in a series of reconstructed tropical ecosystems. Pages 98–108 in *American Society for Photogrammetry and Remote Sensing, 1992 Annual Meeting*, Albuquerque, New Mexico, USA.
- Good, N. F., and R. E. Good. 1972. Population dynamics of tree seedlings and saplings in a mature eastern hardwood forest. *Bulletin of the Torrey Botanical Club* **1972**:172–178.
- Haggard, J. P., and J. J. Ewel. 1994. Experiments on the ecological basis of sustainability: early findings on nitrogen, phosphorus, and root systems. *Interciencia* **19**:347–351.
- Hammel, B. A. 1986a. The vascular flora of La Selva Biological Station, Costa Rica, *Cecropiaceae*. *Selbyana* **9**:192–195.
- . 1986b. The vascular flora of La Selva Biological Station, Costa Rica, *Moraceae*. *Selbyana* **9**:243–259.
- Hartshorn, G. S. 1980. Neotropical forest dynamics. *Biotropica* **12** (Supplement):23–30.
- Hubbell, S. P., and R. B. Foster. 1986. Biology, chance, and history and the structure of tropical rain forest communities. Pages 314–329 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York, New York, USA.
- Hubbell, S. P., and R. B. Foster. 1992. Short-term dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. *Oikos* **63**:48–61.
- Huston, M. A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge, UK.

- King, D. A. 1991. Correlations between biomass allocation, relative growth rate, and light environment in tropical forest saplings. *Functional Ecology* **4**:485–492.
- . 1995. Influence of light level on the growth and morphology of saplings in a Panamanian forest. *American Journal of Botany* **81**:948–957.
- Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**:419–428.
- Kobe, R. K. 1996. Interspecific variation in sapling mortality and growth predicts geographic variation in forest composition. *Ecological Monographs* **66**:181–201.
- Kobe, R. K., and K. D. Coates. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Canadian Journal of Forest Research* **27**:227–236.
- Kobe, R. K., S. W. Pacala, J. A. Silander, Jr., and C. D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* **5**:517–532.
- Leigh, E. G., Jr. 1985. Introduction: why are there so many kinds of tropical trees? Pages 63–66 in E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C., USA.
- Lieberman, M., D. Lieberman, R. Peralta, and G. S. Hartshorn. 1995. Canopy closure and the distribution of tropical forest tree species at La Selva, Costa Rica. *Journal of Tropical Ecology* **11**:161–178.
- McDade, L. A., and G. S. Hartshorn. 1994. La Selva Biological Station. Pages 6–14 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors. *La Selva: ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago, Illinois, USA.
- Myers, R. H. 1990. *Classical and modern regression with applications*. Second edition. The Duxbury Advanced Series in Statistics and Decision Sciences. PWS Kent Publishing Company, Boston, Massachusetts, USA.
- Orians, G. H. 1982. The influence of tree-falls in tree species richness. *Tropical Ecology* **23**:255–279.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, Jr., R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: II Estimation, error analysis, and dynamics. *Ecological Monographs* **66**:1–43.
- Pacala, S. W., C. D. Canham, J. A. Silander, Jr., and R. Kobe. 1994. Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research* **24**:2172–2183.
- Popma, J., and F. Bongers. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* **75**:623–632.
- Popma, J., F. Bongers, M. Martinez-Ramos, and E. Veneklaas. 1988. Pioneer species distribution in treefall gaps in neotropical forest; a gap definition and its consequences. *Journal of Tropical Ecology* **4**:77–88.
- Primack, R. B., P. S. Ashton, P. Chai, and H. S. Lee. 1985. Growth rates and population structure of Moraceae trees in Sarawak, East Malaysia. *Ecology* **66**:577–588.
- Rich, P. M., D. B. Clark, D. A. Clark, S. F. Oberbauer. 1993. Long-term study of solar radiation regimes in a tropical wet forest using quantum sensors and hemispherical photography. *Agricultural and Forest Meteorology* **65**:107–127.
- Ricklefs, R. E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. *American Naturalist* **111**:376–381.
- Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. *Akaike Information Criterion Statistics*. D. Reidel (Kluwer Academic), Boston, Massachusetts, USA.
- Sheil, D., and R. M. May. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* **84**:91–100.
- Strauss-Debenedetti, S., and F. A. Bazzaz. 1991. Plasticity and acclimation to light in tropical Moraceae of different successional positions. *Oecologia* **87**:377–387.
- Swaine, M. D., and T. C. Whitmore. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* **75**:81–86.
- Szymura, J. M., and N. H. Barton. 1986. Genetic analysis of a hybrid zone between the fire-bellied toads near Cracow in southern Poland. *Evolution* **40**:1141–1159.
- van der Meer, P. J., F. Bongers, L. Chatrou, and B. Riéra. 1994. Defining canopy gaps in a tropical rain forest: effects of gap size and turnover time. *Acta Oecologia* **15**:701–714.
- Walters, M. B., E. L. Kruger, and P. B. Reich. 1993. Growth, biomass distribution and CO<sub>2</sub> exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. *Oecologia* **94**:7–16.
- Welden, C. W., S. W. Hewett, S. P. Hubbell, and R. B. Foster. 1991. Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology* **72**:35–40.
- Whitmore, T. C. 1989. Canopy gaps and the two major groups of forest trees. *Ecology* **70**:536–538.