

# Landscape-scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rain forest

David B. Clark, Deborah A. Clark, Paul M. Rich, Stuart Weiss, and Steven F. Oberbauer

**Abstract:** Light is a key resource controlling tree regeneration in the understory of closed-canopy old-growth forests. To evaluate the distribution of understory light environments at a landscape scale, we used stratified random sampling in a 500-ha stand of Costa Rican tropical rain forest. Fifteen 100 m long transects were placed using random coordinates within two soil-geomorphology units (flat alluvial terraces and dissected ridge-slope-swale terrain). At 2.5-m intervals we measured canopy height and slope angle, classified topographic position, and took canopy photographs with a fish-eye lens at 1 and 3 m above the ground (and at 0.6 and 5 m height at five stations per transect). Photographs were analyzed for global site factor (GSF), which is analogous to the percentage of full sun radiation reaching a point. Canopy height and GSF at 1 and 3 m above the ground were significantly autocorrelated (Moran's *I*) at 2.5-m intervals. The autocorrelation rapidly declined at greater intervals, reaching nonsignificance at ca. 20 m. Both canopy height and GSF at 3 m height had a weak tendency for negative autocorrelations at intervals of 25–50 m. Median canopy height (615 stations) was 23 m (range 0–37). Gaps (canopy height  $\leq 2$  m, Brokaw 1982) were only 1.5% of sample points. Gaps were more frequent on steep slopes than on terraces, ridgetops, swales, and gentle slopes. Canopy height varied significantly across this topographic gradient. At all four heights (0.6, 1, 3, and 5 m) median GSF was  $\leq 2.4\%$ . GSF values  $>8\%$  accounted for only 3% of the total sample ( $N = 1380$ ). GSF was only weakly negatively correlated with canopy height and the relation was not monotonic. Under canopies 13–19 m tall, nearly all GSF values were  $\leq 5\%$ . Higher GSFs were more frequent under both shorter and taller canopies. Given the observed variance in GSF and canopy height, 100–200 points separated by intervals of  $\geq 20$  m are necessary to measure the forest-wide means of these variables to  $\pm 10\%$ . We discuss implications of these results for current approaches to modeling understory light based on canopy characteristics. We compared the random background of light environments from 1–3 m above the ground at La Selva with those occupied by saplings of pioneer and nonpioneer tree species. The two pioneers (*Cecropia* spp.) occurred in microsites significantly brighter than random sites, while sapling microsites of all five nonpioneer species were significantly darker than random. Comparing the landscape-scale distribution of key resources with species' actual distributions at similar scales offers a quantitative method for assessing plant life histories within and among forests.

**Résumé :** La lumière est une ressource-clé qui régit la régénération des arbres en sous-étage de la voûte fermée des forêts primitives. Afin d'évaluer sa distribution en sous-étage, on a utilisé un échantillonnage aléatoire stratifié dans un peuplement de 500 ha d'une forêt tropicale ombrophile du Costa Rica. Quinze transects d'une longueur de 100 m ont été placés à l'aide de coordonnées aléatoires dans deux unités de sol-géomorphologie (terrasses alluviales planes et terrain découpé de crête, pente et dépression). On a mesuré, à des intervalles de 2,5 m, la hauteur de la voûte et l'angle de la pente, classé la position topographique et photographié la voûte à l'aide d'un objectif à 180°, à 1 et à 3 m au-dessus du sol (et à 0,6 et à 5 m de hauteur dans cinq stations par transect). Les photographies ont été analysées pour déterminer le facteur global du site (FGS) qui est analogue au pourcentage de la radiation solaire maximale atteignant un point. La hauteur de la voûte et le FGS à 1 et

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**D.B. Clark<sup>1</sup> and D.A. Clark.** Department of Biology, University of Missouri – St. Louis, 8001 Natural Bridge Road, St. Louis, MO 63121-4499, U.S.A.

**P.M. Rich.** Biological Sciences, University of Kansas, Lawrence, KS 66054-2106, U.S.A.

**S.Weiss.** Center for Conservation Biology, Stanford University, Stanford, CA 94305, U.S.A.

**S.F. Oberbauer.** Department of Biological Sciences, Florida International University, University Park, Miami, FL 33199, U.S.A., and Fairchild Tropical Garden, 11935 Old Cutler Road, Miami, FL 33156, U.S.A.

<sup>1</sup> Author to whom all correspondence should be addressed. Present address: La Selva Biological Station, Interlink-341, P.O. Box 02-5635, Miami, FL 33152, U.S.A.

à 3 m du sol étaient autocorrélés de façon significative ( $I$  de Moran) à 2,5 m d'intervalle. L'autocorrélation a rapidement décliné aux intervalles plus grands, perdant toute signification à environ 20 m. À 3 m du sol, tant la hauteur de la voûte que le FGS montraient une faible tendance à s'autocorréler négativement à des intervalles de 25 à 50 m. La hauteur médiane de la voûte (615 stations) était de 23 m (étendue de 0 à 37 m). Les ouvertures (voûte d'une hauteur  $\leq 2$  m, Brokaw 1982) ne représentaient que 1,5% des points échantillonnés. Elles étaient plus fréquentes sur les pentes abruptes que sur les terrasses, les crêtes, les dépressions et les pentes douces. En rapport avec ce gradient topographique, la hauteur de la voûte variait de façon significative. À chacune des quatre hauteurs (0,6, 1, 3 et 5 m), le FGS médian était  $\leq 2,4\%$ . Les valeurs du FGS  $> 8\%$  ne comptaient que pour 3% de l'échantillon total ( $N = 1380$ ). Le FGS n'était corrélé négativement que faiblement avec la hauteur de la voûte et la relation n'était pas monotonique. Sous les voûtes de 13 à 19 m de hauteur, presque toutes les valeurs du FGS étaient  $\leq 5\%$ . Les valeurs plus élevées du FGS étaient plus fréquentes sous les voûtes plus basses comme sous les voûtes plus hautes. Selon la variance observée du FGS et de la hauteur de la voûte, 100 à 200 points séparés par des intervalles  $\geq 20$  m sont nécessaires pour mesurer les moyennes de ces variables à la grandeur de la forêt à  $\pm 10\%$ . L'implication de ces résultats, utiles aux démarches courantes de la modélisation de la lumière en sous-étage, a été discutée sur la base des caractéristiques de la voûte. À La Selva, on a comparé les antécédents aléatoires des environnements lumineux de 1 à 3 m du sol à ceux occupés par les gaules d'espèces ligneuses pionnières et non pionnières. Les deux espèces pionnières (*Cecropia* spp.) sont apparues dans les microsites significativement plus éclairés que les sites aléatoires, alors que les microsites des gaules des cinq espèces non pionnières étaient significativement plus sombres que les microsites aléatoires. La comparaison du niveau de distribution des ressources-clés à l'échelle du paysage avec la distribution actuelle des espèces aux échelles similaires offre une méthode quantitative pour évaluer le cycle vital des plantes à l'intérieur d'une forêt et entre les forêts.

[Traduit par la Rédaction]

## Introduction

In the understories of old-growth closed-canopy forests, light is frequently a limiting resource for plants. Intuitively, it seems reasonable that the tree species composition of a forest landscape should be related to the frequency distribution of sapling light environments (Denslow 1980). Forests with high frequencies of large gaps, for example, should have more species dependent on high-light sites for regeneration.

To address this hypothesis requires measuring the frequency distribution of light environments at a scale appropriate to species-level analyses. Simply knowing the frequency distribution, however, is likely to be insufficient for a comparative analysis of plant life history patterns. Understory light environments are affected by many factors, including overstory species composition, successional stage, local patch history, and the slope, aspect, latitude, and climate of the site (Terborgh 1985; Canham et al. 1990, 1994). Similar distributions of understory light environments in different forests may result from different combinations of these variables. For this reason it is desirable to know not only the frequency distribution of light levels in the understory, but also how these levels are related to structural aspects of the site.

In this paper we present a procedure for estimating understory light environments, and their relation to forest structure and site topography, at scales applicable to plant life history analyses. We also use existing data on the light microsites of saplings of seven canopy tree species from the same forest to demonstrate the application of this type of landscape-scale data to analysis of tree regeneration patterns.

The landscape where we developed and tested these methods is an old-growth lowland tropical rain forest. Most previous investigations of tropical rain forest understory light environments (including our own) have focused

on a few sites subjectively chosen by investigators to represent understory conditions in tree-fall gaps or mature-phase forest (cf., Chazdon and Fetcher 1984; Turton 1988; Denslow et al. 1990; Dirzo et al. 1992; Brown 1993; Rich et al. 1993; Whitmore et al. 1993). From these studies it is not possible to determine whether the sites selected were in fact representative of the selected microsite types, or to evaluate the relative frequency of such microsites at the landscape scale.

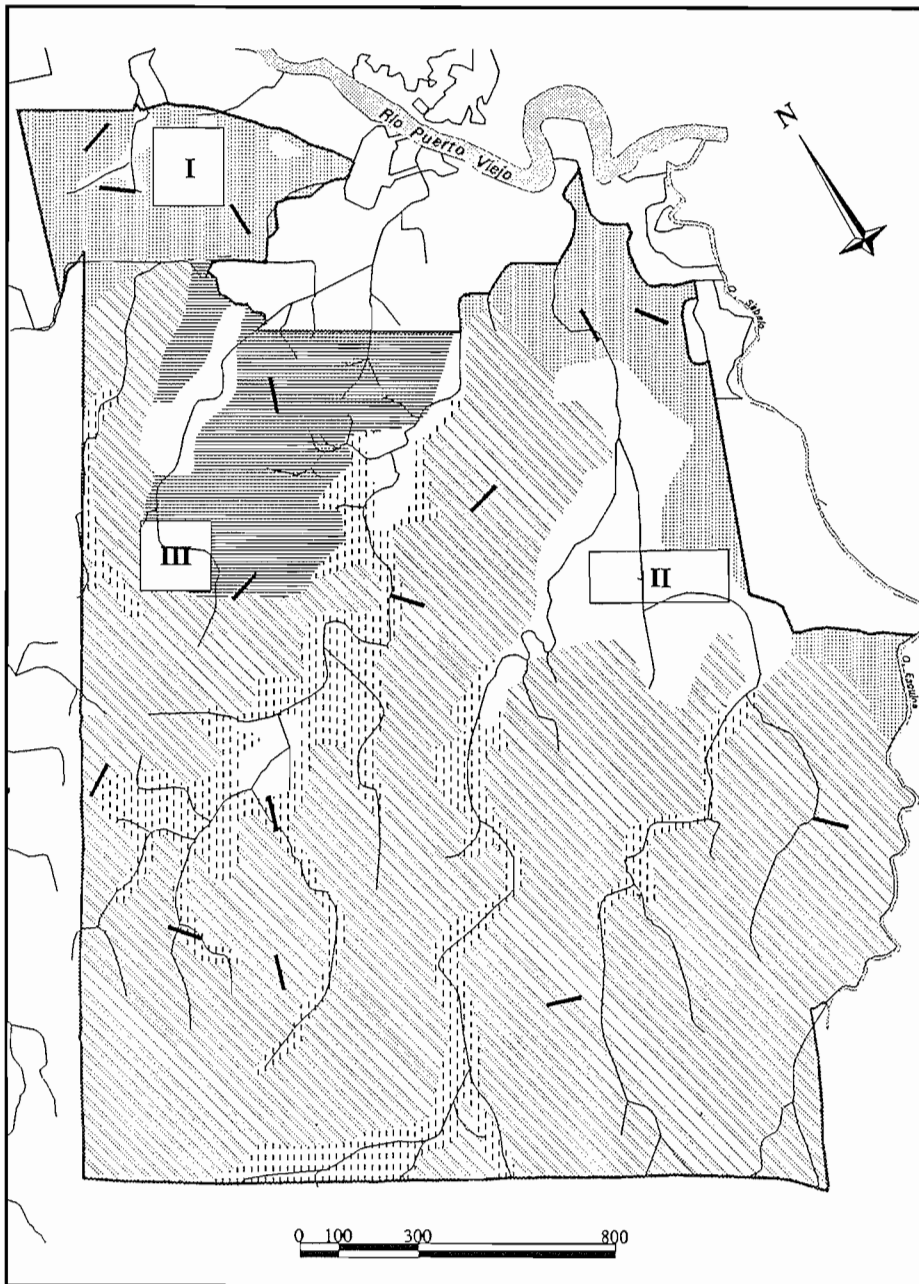
Scaling up from spatially restricted samples to entire landscapes will require new approaches to sampling (Botkin and Simpson 1990; Caldwell et al. 1993). Becker and Smith (1990) pioneered one such approach to characterizing understory light environments at landscape scales. Using two 1 km long transects, they measured the forest-level frequency distribution of, and spatial autocorrelation among, understory light environments in a tropical moist forest. Building on these ideas, we carried out a landscape-scale assessment of light environments and forest structure in a 500-ha stand of old-growth lowland tropical rain forest. Our primary goal was to obtain unbiased estimates of the magnitude and distribution of understory light environments at the landscape scale, and to compare these light environments with those occupied by canopy tree saplings. We were additionally interested in the relation of these light environments to forest structure and site conditions. The data we present come from one particular forest, but the methods and analyses are applicable to any forested landscape.

## Methods

### Study site

The study was carried out at the La Selva Biological Station of the Organization for Tropical Studies in Costa Rica (10°26'N, 83°59'W). The old-growth forest is classified as Tropical Wet

**Fig. 1.** Location of the study area and transect locations within the nonswamp old-growth forest at the La Selva Biological Station, Costa Rica. Shaded areas were sampled; areas in white (swamps, developed or restricted areas, second growth) were excluded. The dissected topography area consisted of ridge and slope areas (diagonal hatching), streamside areas (vertical dashes) and the Arboleda series (horizontal hatching). The second topographic unit, old alluvial terraces, is indicated with vertical stippling. Solid lines indicate the transects, which were sited within the two geomorphological units by the use of randomly drawn azimuths and  $x$ - $y$  coordinates. Scale bar is in metres.



Forest in the Holdridge system (McDade and Hartshorn 1994). Rainfall is ca. 4000 mm/year, and no month receives <100 mm on the average (Sanford et al. 1994). A complete description of the site is given in McDade et al. (1994).

Because our focus was on the light environments of non-swamp old-growth forest, we limited our sample area to a core

567-ha section of the reserve (Fig. 1). Within the 567 ha we excluded swamp forests (55 ha) and restricted access plots (an additional 10 ha); thus the area sampled was 502 ha. The starting coordinates and azimuths for fifteen 100 m long transects were generated by a random number program. The randomly selected start points were located by reference to the

nearest grid post of the La Selva 50 × 100 m grid. Potential transect routes that crossed swamps, trails, or restricted access areas were discarded. Sampling was stratified by two soil-geomorphology categories (see Sollins et al. 1994 for further descriptions of these areas): flat, relatively fertile old alluvial terraces, which covered 58 ha (5 transects), and areas of undulating terrain with short but steep slopes on poorer soils (10 transects). Areas mapped as the Arboleda soil series, which may be overlain by old alluvial deposits but are on dissected topography (data in Clark et al. 1995), were grouped with the poorer soils, as were the streamside soils in this area (combined area = 444 ha).

### Transect sampling and analysis techniques

Measurements were taken at sample points every 2.5 m along each transect. At each sample point the height of the highest leaf directly above the point was assessed using an optical range finder (Ranging Inc. model 620). If no vegetation was present over the point, the canopy height was recorded as zero. The range finder was calibrated daily ( $\pm 1$  m) using two horizontal bench marks. A clinometer was used to establish verticality. In practice, it was frequently necessary to move several steps from the sample point to obtain a clear view of the highest canopy directly overhead. In these cases care was taken to remain at the same elevation as the sample point, and to insure that the same branch was being sighted.

Slope angle at each sample point was measured over a distance of 2 m in the direction of greatest slope by sighting with a clinometer between two 1.5 m tall staffs each placed 1 m from the sampling point (one upslope and one downslope from the point). Topographic position at each station was categorized as (i) level ridgetop or upland alluvial terrace; (ii) gentle to moderate slope; (iii) steep slope; (iv) swale or riparian site.

At every sample point fish-eye canopy photographs were taken at 1 and 3 m above the ground using a 35-mm camera with a Nikkor 8-mm hemispherical lens mounted in self-leveling gimbals. In addition, photographs were taken at 0.6- and 5-m heights at the stations located at 20, 40, 60, 80, and 100 m along each transect. The gimbals were mounted on a tripod (measurements at 0.6-m height), a monopod (measurements at 1- and 3-m height), or a monopod with a 3-m extender and a long remote release (measurements at 5-m height).

Photographic negatives were input to a digitizer from a videocamera and analyzed using the program CANOPY (Rich 1990). Direct site factor (DIRsf: the proportion of potential direct light at a site relative to a site in the open) and diffuse site factor (DIFsf: the proportion of potential diffuse light at 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 estimates of DIRsf matched within 0.005 units. Analyses by the two different operators were then adjusted to the same standard using slopes and intercepts from calibrations on a standard set of photographs. Direct and diffuse site factors were combined into a global site factor (GSF) using the equation

$$\text{GSF} = 0.45(\text{DIRsf}) + 0.55(\text{DIFsf})$$

These weighting factors have been found to maximize the correlation of GSF values with long-term measurements of photosynthetically active radiation (PAR) in the understory at La Selva (Rich et al. 1993). Global site factor, thus weighted, corresponds with the percentage of total PAR reaching a site relative to a site in the open. We compared GSF data from this study with existing data on the distribution of saplings' crown light environments to determine how the regeneration of canopy tree species at La Selva relates to the background availability of light microsites. The sapling data include all individuals 1–3 m tall of seven tree species studied by Clark et al. (1993)

(two species with sample sizes <5 were excluded from this analysis). To obtain a random "background," we used the data from six stations per transect, each separated by 20 m, and averaged the 1- and 3-m values to obtain an estimate of the random expectation of light environments between 1 and 3 m above the ground.

### Statistical analyses

We investigated spatial patterns of understory light environments and canopy height at two different scales: relations among sample points at distances from 2.5 to 50 m and comparisons between large areas of different soil and topography. To examine small-scale spatial structure, we calculated Moran's *I* for each transect at different intervals between points. Moran's *I* is a measure of autocorrelation that is analogous to Pearson's correlation coefficient (Sokal and Thomson 1987). It usually varies from 1 to -1 depending on the autocorrelation of pairs of points separated by a given distance interval. Based on the results of these analyses, we subsampled the transects at intervals greater than the significant autocorrelation zones (20 m) to obtain independent samples at each transect location. There were therefore 6 independent samples per transect (stations 0, 20, 40, 60, 80, and 100 m), except for the GSF analysis at 0.6 and 5 m, which was based on five independent observations per transect. Differences between the two geomorphological areas were analyzed using nested ANOVA with areas as the highest factor and transects nested within areas, using the six subsampled points per transect.

### Precision of the methods

We evaluated the precision of the methods by remeasuring all variables for one transect after a brief interval. This transect was first measured on 29 and 30 July 1992 and was remeasured on 7–10 August 1992. For both canopy height and slope angle, the median difference in remeasurements was zero ( $N = 41$ ). Topographic position categorizations were highly repeatable; 95% of the values were identical. The median absolute differences between consecutive GSF measurements at 0.6, 1, 3, and 5 m above the ground were, respectively, 0.4, 0.6, 1.0, and 0.7% ( $N = 5, 41, 41, \text{ and } 5$  pairs of repeated measurements).

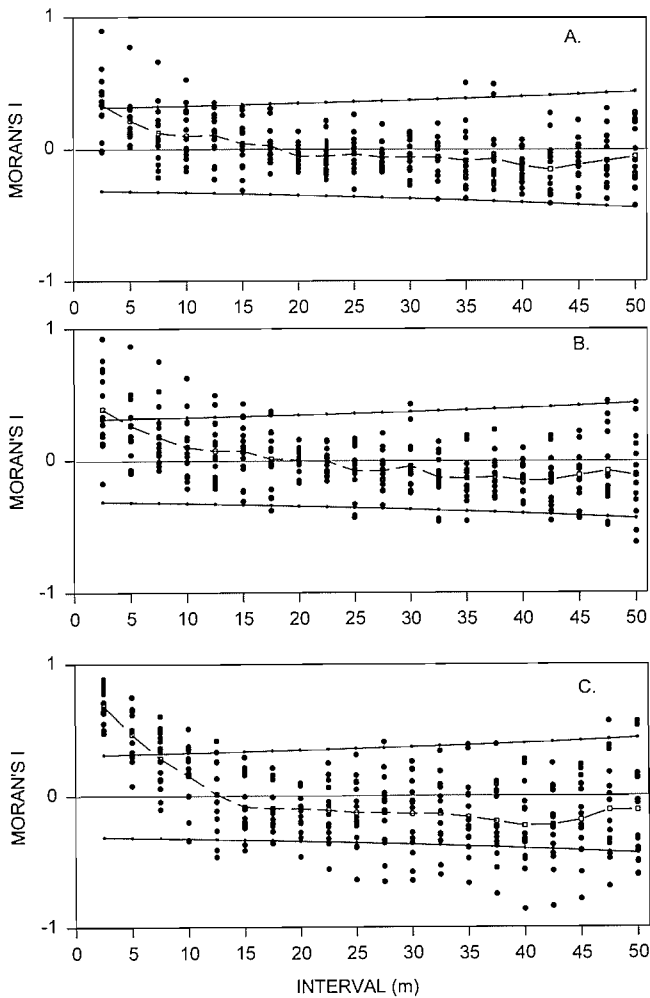
## Results

### Small-scale structure of light environments and canopy height

Global site factors were significantly autocorrelated with the smallest spatial scale (2.5 m distance). For GSF at 1-m height (Fig. 2A), however, only 1 or 2 autocorrelations were significant at intervals of 5–12.5 m along the transects, and none was significant for intervals of 15–30 m. For GSF at 3-m height (Fig. 2B) the pattern was similar, but there were more significant positive autocorrelations for intervals of 5–17.5 m (15 of 90 for GSF at 3-m height, compared with 7 of 90 for GSF at 1-m height). There was a tendency towards negative autocorrelations between sample points spaced 25–50 m apart. At intervals of 27.5–50 m, 116 of the 150 correlations were negative, 10 of them significantly (Fig. 2B).

Canopy height (Fig. 2C) was strongly autocorrelated between adjacent sample points (2.5 m apart) along the transects. At each of the intervals 5, 7.5, and 10 m, 4–11 of the 15 values of Moran's *I* were significant. At intervals of 15–25 m, only 1–3 of the 15 autocorrelations were

**Fig. 2.** Spatial autocorrelation (Moran's  $I$ ) at increasing intervals along the fifteen 100 m long transects. Solid external lines indicate the 95% confidence intervals for each autocorrelation (calculations follow Legendre and Legendre 1983, p. 349). The broken central line connects means (open squares) of the 15 autocorrelations at each interval distance (one per transect). Sample sizes decrease by one per interval, from  $N = 40$  at 2.5 m to  $N = 21$  at 50 m. (A) Global site factor (i.e., estimated percent full sun, see Methods) at 1 m above ground. (B) Global site factor at 3 m above ground. (C) Canopy height.



significant, and the mean autocorrelation was close to zero. From 27.5 to 50 m the mean autocorrelation was also close to zero, but there were many more significant negative correlations than expected by chance alone (32 of 150 were significantly negative at  $P = 0.05$ ). In summary, canopy heights tended to be significantly and positively correlated at distances  $<15$  m, weakly and negatively correlated at distances of 25–50 m, and not significantly correlated at points separated by 15–25 m.

Based on these patterns of forest height and GSF, we chose to subsample at 20-m intervals for analyses requiring independent samples along each transect. At this sample interval, 44 of 45 autocorrelations of canopy height and of GSF at 1 and 3 m were not significant, and the mean

**Table 1.** Descriptive statistics of global site factor, an estimate of the percentage of available light relative to a site in the open, at four heights above the ground, 15 transects combined.

	Height above ground (m)			
	0.6	1	3	5
Mean	2.3	2.1	2.9	4.1
Median	1.9	1.9	2.3	2.4
Min.	0.3	0.1	0.2	0.3
Max.	11.9	14.2	20.4	28.6
CV	79.4	65.3	85.1	118.8
$N$	75	615	615	75

autocorrelation for each variable was very close to zero for all of the 15 transects.

#### Magnitude of available light

At all four heights above the ground, median GSF values were  $<3\%$  (Table 1, Fig. 3). The range, variability, and maximum values of light levels all increased with increasing height (Table 1). Sites with GSF  $>8\%$  accounted for only 3% of the total sample (all heights together,  $N = 1380$  photographs), although at 5 m above the ground 11% of the stations ( $N = 75$ ) had GSF values this high (Fig. 3). Global site factors at 1 and 3 m above the ground did not differ between geomorphological types (nested ANOVA, two types (1 df), 15 transects (13 df), six samples per transect (75 df),  $P = 0.889, 0.643$  for 1- and 3-m GSF).

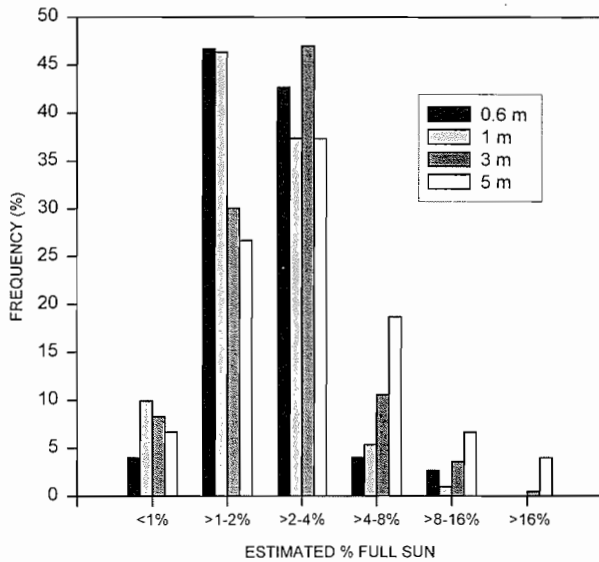
Median GSF increased significantly with height above the ground at the 75 stations where GSF was measured at all four heights (at 0.6, 1, 3, and 5 m from the ground, Friedman two-way,  $P < 0.001$ ). The median GSF levels at 0.6 and 5 m above the ground were 1.9 and 2.4%, an increase of only 0.5%. Nevertheless, because the GSF levels are so low at 0.6 m, this represented a median increase of ca. 32% in GSF over this height range at each point.

#### Canopy height and topography

The median height of the upper surface of the forest was 23.0 m ( $N = 615$ ,  $\bar{x} = 21.9$  m, range 0–37 m). About half of the canopy surface is between 20 and 30 m above the ground (Fig. 4). Gaps, defined as vertical openings extending from  $\leq 2$  m above the ground to the sky (Brokaw 1982), accounted for only 1.5% of the locations sampled. Median canopy height varied from 16 to 30 m among transects. There was no significant difference in canopy height between flat alluvial areas and dissected topography areas (nested ANOVA, two habitat types (1 df), 15 transects (13 df), six samples per transect (75 df),  $P = 0.854$ ).

The transects on old alluvial terraces were flat, averaging only  $6^\circ$  slope. In contrast, transects on dissected terrain averaged  $14^\circ$ , with 13% of points on slopes over  $25^\circ$ . Topographic position varied similarly. None of the 205 sites on alluvial terraces were categorized in the fieldwork as steep slopes, whereas 22.2% of the dissected terrain sites

**Fig. 3.** Frequency distribution of estimated percent full sun values (i.e., global site factors, see Methods) at different heights above the ground. Data are for all 15 transects combined.  $N$  (points) at 1 and 3 m = 615; at 0.6 and 5 m = 75.



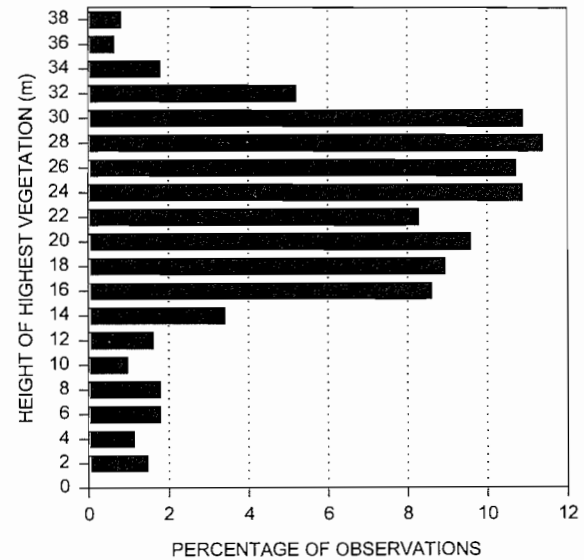
were (mean slope of these 91 sites = 25°). Riparian and swale habitats were much more common on the dissected terrain than on alluvial terraces (21.2% vs. 4.4%), reflecting the comparative frequency of small streams and inter-ridge valley bottoms.

Canopy height varied among topographic positions (Kruskal-Wallis ANOVA among the four topographic positions for 90 subsampled points,  $P = 0.03$ ); median canopy heights ranged from 21.5 m for sites on steep slopes to 27.5 m for sites in swales. Sites with canopies  $\leq 5$  m above the forest floor (therefore current or recent gaps) were three times more common on steep slopes (7.7%, 7/91 stations) than on the other three topographic positions combined (2.5%, 13/524 stations). Canopy height was not significantly correlated with slope angle ( $N = 90$ ,  $r^2 = 0.01$ ).

#### Relationship between light availability and canopy height

Figure 5 illustrates the complex relations between canopy height and light environments 1 and 3 m above the ground in La Selva's old-growth forest. The transect with the lowest coefficient of variation in canopy height (Fig. 5A) is within a  $\geq 100$  m long section of forest where mean canopy height was  $>20$  m. The understory was uniformly dark; most stations had 1- and 3-m GSFs of  $<4\%$ . Fig. 5B shows a transect with an intermediate coefficient of variation in canopy height. A 5 m wide gap penetrates almost to ground level at 20–22.5 m along the transect but is not accompanied by markedly increased GSFs. GSF values at 3 m above the ground are as high or higher than in this gap at four stations along the transect where the canopy is  $>25$  m tall. Fig. 5C shows the transect with the highest coefficient of variation in canopy height. A small gap (sensu Brokaw 1982) is evident at 10–12.5 m along the transect,

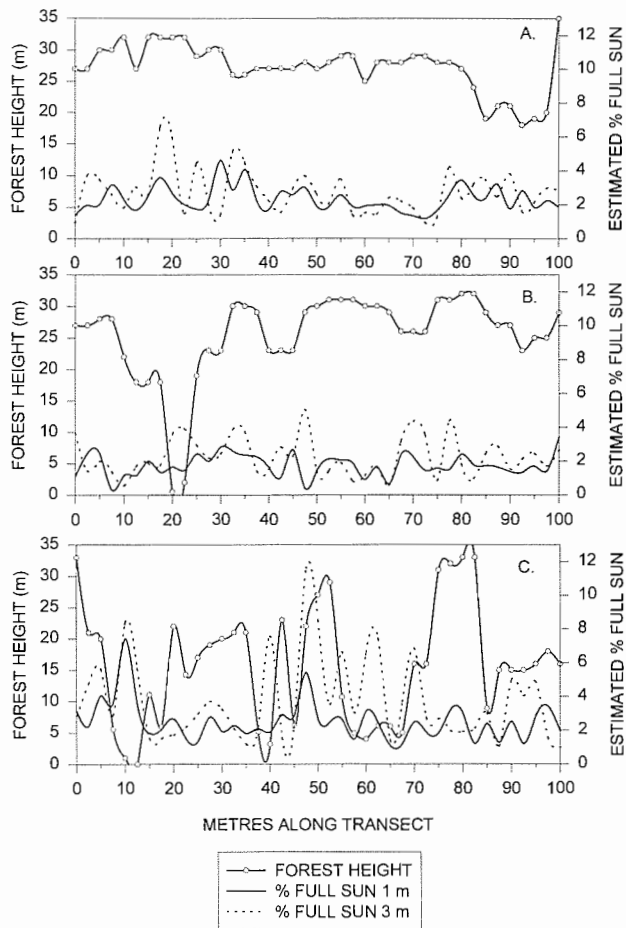
**Fig. 4.** Frequency distribution of canopy height in old-growth nonswamp forest at La Selva Biological Station. Data points are from 615 sample stations on fifteen 100 m long transects sampled every 2.5 m. Y-axis values are inclusive upper class limits (e.g., 2 = 0 to  $\leq 2$  m).



and the 1- and 3-m GSFs both rise to ca. 8% in this area. The general inverted cone shape of tropical moist forest gaps (Hubbell and Foster 1986) is evident in this gap and several others along this transect. There are several areas of canopy  $<15$  m tall, and most are associated with 2 to 3-fold increases in understory GSF levels. Note, however, that the highest GSF ( $>11\%$  at 47.5 m) is under forest canopy  $>20$  m high and is 2.5 m to the right of the 7-m canopy at the 45-m station. This offset may be due to lateral light penetrating the understory from the adjacent gap.

At all four heights above the ground, GSF was weakly and negatively correlated with the height of the local forest canopy. Considering the 75 sample points with measurements at four heights (five sample points per transect  $\times$  15 transects), Pearson's  $r$  between GSF and canopy height was  $-0.30$ ,  $-0.30$ ,  $-0.46$ , and  $-0.45$ , at 0.6, 1, 3, and 5 m above the ground, respectively (all  $P < 0.01$ ). The data, however, show a non-monotonic trend in this relationship. Figure 6 shows the distribution of the entire GSF data set (GSF at 1- and 3-m heights,  $N = 615$  for each; GSF at 0.6- and 5-m heights,  $N = 75$  for each). Under forest canopy 13–19 m high, only 1 of 302 measurements (0.3%) at any level in the understory had a GSF  $>5\%$ . In contrast, 25% of measurements ( $N = 144$ ) under canopy  $<13$  m high had GSF values above 5%, and under forest  $>19$  m tall 6% of measurements ( $N = 934$ ) had GSF values over 5%. We interpret the 13–19-m zone of canopy heights as densely foliated, regenerating gaps. Evidently in these areas of this forest, penetration of significant amounts of light to the understory is extremely rare. Under canopies  $<13$  m tall, sites with high light in the understory can be due to either overhead or lateral light, while under canopies  $>19$  m tall, all understory sites with high light are illuminated by lateral lighting.

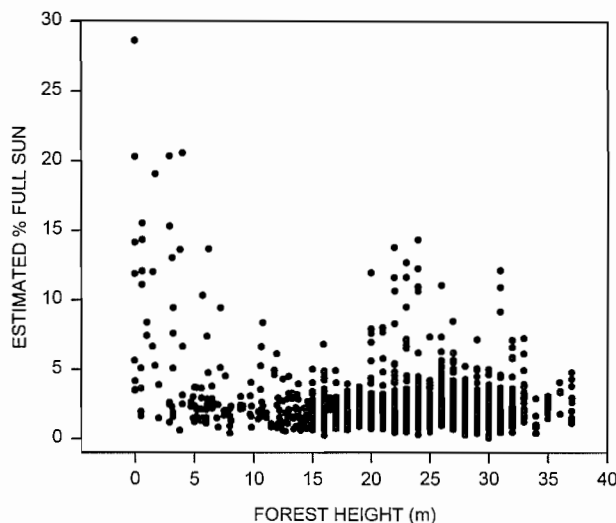
**Fig. 5.** Canopy height and estimated percent full sun (i.e., global site factor, see Methods) at 1 and 3 m above the ground along the transect with (A) the lowest coefficient of variation (CV) of canopy height (14%); (B) an intermediate CV of canopy height (27%); and (C) the highest CV of canopy height (60%).



### Light environments and tree regeneration in the understory

We compared the random background of understory light environments between 1 and 3 m (see Methods) with those occupied by 1–3 m tall saplings of seven canopy tree species (further described in Clark et al. 1993). Two of the tree species are pioneers (*sensu* Swaine and Whitmore 1988) in the genus *Cecropia*. Compared with the background distribution of light environments (Fig. 7), sapling microsites of both *Cecropia* species were markedly right-shifted (Mann–Whitney  $U$  two-sample test between background and sapling distributions, two-tailed  $P \leq 0.01$  for both species). More than half of the 1–3 m tall *Cecropia* saplings occurred in sites with GSF >8%, while such sites made up only 3% of the background distribution. These two pioneer species have specialized on a low-frequency but high-energy portion of the light microsite gradient. For the five nonpioneer species, which represent a range of life history patterns (Clark and Clark 1992), the situation was reversed. All these species occurred in significantly darker microsites than the random background (Fig. 7; for

**Fig. 6.** Distribution of estimated percent full sun values (i.e., global site factors, see Methods) from all transects with respect to canopy height. Data from 0.6, 1, 3, and 5 m above ground are combined.  $N = 1380$ .



each species, Mann–Whitney  $U$  two-sample test between background and sapling distributions, two-tailed  $P < 0.01$ ).

## Discussion

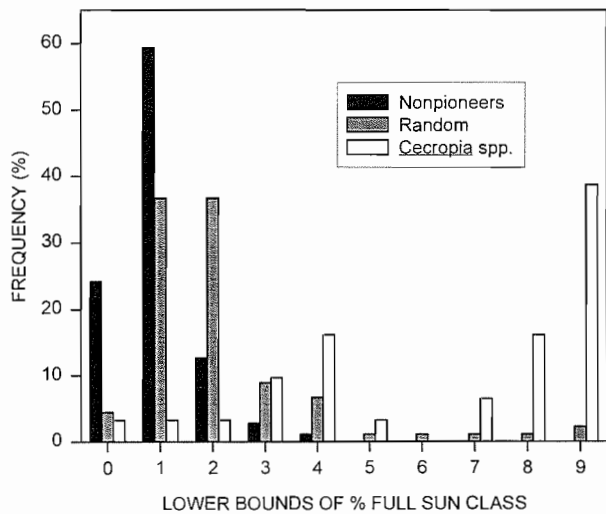
### Tropical rain forest understory light environments

Light environments in gaps and closed-canopy understory have previously been measured in several tropical wet and moist forests (cf. La Selva, Costa Rica: Chazdon and Fetcher 1984; Barton et al. 1989; Canham et al. 1990; Denslow et al. 1990; Ellison et al. 1993; Rich et al. 1993; Queensland, Australia: Turton 1988, 1992; Barro Colorado Island, Panama: Becker and Smith 1990; Smith et al. 1992; Los Tuxtlas, Mexico: Dirzo et al. 1992; Danum Valley, Sabah: Whitmore et al. 1993). In spite of the differences in methods and analysis techniques, the data are reasonably consistent. Sites near ground level subjectively judged as good understory in these forests receive about 1–5% of the photosynthetically active radiation (PAR) reaching sites in the open. Values from fully exposed sites in gap centers range, depending on gap size, from ca. 5 to 40% of full-sun PAR.

Our data on the forest-wide distribution of light environments at La Selva are broadly consistent with these findings. Median GSF at sites with canopy heights  $\leq 2$  m (gaps by any current definition) was 5.3% ( $N = 9$ ), while median GSF at sites with canopies >30 m tall was 1.9% ( $N = 82$ ). However, our data also show that microsites with >5% GSF are very infrequent in the La Selva understory. Only 3% of the 615 GSF measurements at 1 m above the ground were >5%, and only 1% were >10%. While sites receiving 20–40% of full-sun PAR do exist in La Selva old growth (presumably in the centers of very large gaps), they are extremely scarce at the landscape scale.

Our study by design avoided subjective classifications of gap or mature-phase patches. Because we sampled the landscape at random, the data are generalizable to large landscape units. The only other studies that we are aware

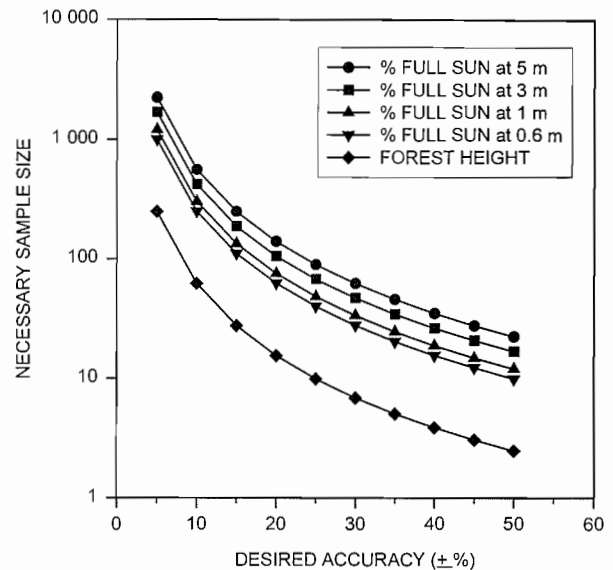
**Fig. 7.** Comparison of the distribution of the random background levels of percent full sun values (i.e., global site factors (GSF) see Methods) between 1 and 3 m above the ground in old-growth upland forest at La Selva and GSF measured over the crowns of 1–3 m tall saplings of five nonpioneer tree species and two pioneer species in the same forest. Data for background light levels are mean GSF values from 1 and 3 m above the ground (measurements at both heights averaged for all stations separated by 20 m within transects ( $N = 90$  stations total; this study)). Data for the saplings were taken from Clark et al. (1993). The five nonpioneer species (with sample sizes) were *Dipteryx panamensis* (28), *Lecythis ampla* (42), *Miconia guianensis* (36), *Pithecellobium elegans* (23), and *Simarouba amara* (53). The pioneer species (with sample sizes) were *Cecropia obtusifolia* (23) and *Cecropia insignis* (8).



of that have adopted this approach are Becker and Smith (1990) and Smith et al. (1992) for light environments in a seasonally deciduous forest in Panama. They calculated potential PAR from photographs taken at 0.6 m above the ground along a 1-km transect in a normal (non El Niño) wet season. Estimates of understory PAR were significantly spatially autocorrelated (Moran's  $I$ ) at intervals of 2.5 m, marginally significantly autocorrelated at 5-m intervals, and not correlated at greater intervals. In spite of the substantial differences between La Selva and the Panama forest in rainfall (ca. 4000 and 2700 mm annually, respectively, Gentry 1990) and seasonality (evergreen and semideciduous, respectively), the La Selva GSF data (Fig. 2A) show a very similar pattern. In these two cases (tropical wet forest and fully leafed-out tropical moist forest), understory light environments are extremely spatially variable at relatively small spatial scales. While large patches of low-light environments are common landscape features (e.g., our Fig. 5A), knowledge of the light environment at a given point in the understory gives no statistical power to predict light environments 15–25 m away.

For analysis of spatial patterns in light environments, intensive (small-scale) sampling is required. For such studies, spatial autocorrelation is expected and is itself a variable of interest. In contrast, to compare light environments or

**Fig. 8.** Sample sizes necessary to measure the forest variables evaluated in this study at varying degrees of accuracy (significance level = 0.05), based on the observed means and variances of these variables. Sample means and variances are from the 75 stations (5 per transect) with light measurements at all four heights above the ground (these stations are separated by 20-m intervals and are therefore not autocorrelated; see Results). Note log scale on y axis. Necessary sample sizes were calculated following Eckblad (1991): sample size =  $((t\text{-value})^2(\text{sample variance})/(\text{accuracy} \times \text{sample mean})^2)$ .



canopy height between landscape units, independent samples are required. In this study we arrived at statistically independent samples by subsampling, an inefficient technique (Legendre 1993) that can be avoided once the scale of spatial structure is known. Based on our work and that of Becker and Smith (1990), we suggest that for tropical wet and moist forests, statistical independence can be achieved with sample spacings on the order of 20–25 m. This prediction should be tested in other closed-canopy old-growth forests.

The number of samples necessary to describe structural features of a landscape with a given accuracy is proportional to the variance of the variable of interest (Eckblad 1991). Figure 8 shows that for the La Selva forest, substantially more samples are required to accurately estimate light environments than are needed to measure canopy height. Given all the sources of measurement error in GSF estimates (Rich 1990; also see Methods, this study) and the low absolute values of understory GSF, analyses of GSF distributions will probably involve accepting lower levels of accuracy than studies of canopy height. The results shown in Fig. 8 suggest that on the order of 100–200 independent samples are sufficient to give reasonably accurate estimates of both understory light environments and canopy height in forest such as La Selva.

#### Understory light and canopy structure

Tree saplings are usually light limited in understory sites within closed-canopy old-growth forests (Clark and Clark



1992). This means that a realistic model of forest regeneration must have understory light inputs. Actually measuring understory light at plot to landscape scales, however, is labor intensive. A less laborious alternative is to predict understory light based on canopy characteristics. Our data show that this will not be straightforward in tropical rain forests.

Understory light levels at La Selva are only weakly related to the height of the canopy over a point. At 1-m height, the  $r^2$  for the GSF – canopy height negative correlation was only 0.09. One reason for the low correlation is illustrated in Fig. 5. Penetration of lateral light can produce understory light environments under tall forest canopy that are equivalent to gap light environments. An additional reason is suggested in Fig. 6, which shows a strong constriction in the variance of light values (and uniformly low values) under the 13–19 m tall canopy. These sites, which we believe to be regenerating canopy gaps, are “black holes” of light at ground level. These sites have uniformly dense canopies that consistently block light both vertically and laterally.

Figures 5 and 6 also illustrate the difficulty of modeling understory light levels in relation to canopy height in this old-growth forest. A typical negative-exponential model (such as the Beer–Bouguer law, Botkin 1993), which assumes a regular and reasonably predictive relation between canopy height and understory light, will not fit the relationships documented here. Models based on geometric reconstructions of canopies through species-specific (cf. Canham et al. 1994) or forest-wide (cf. Lieberman et al. 1995) allometric relationships are another possibility. Developing the necessary allometric equations, however, will be a challenge. There are over 300 tree species at La Selva (Hartshorn and Hammel 1994), which is by no means a particularly tree-speciose tropical rain forest. The diameter/height relation is further obscured by the high prevalence of physically damaged stems in tropical rain forests (Putz and Brokaw 1989; Clark and Clark 1991), and by the high incidence of nondicot trees (palms account for 26% of the stems  $\geq 10$  cm at La Selva, Lieberman et al. 1985).

Our results suggest several lines for future efforts to quantify the relation between understory light and canopy structure. The influence of lateral lighting should be examined empirically (as it has been theoretically, Canham et al. 1990). How far does lateral light actually penetrate, and what factors in the field account for variance in this penetration? Sites under the 13–19 m tall canopy were shown here to be uniformly dark; the underlying factors should be investigated. Given their abundance and nondicot architecture, the special role of canopy and subcanopy palms on tropical forest understory light merits attention. Whatever modeling approach is adopted, our data indicate that extensive ground truthing will be necessary to develop predictive relationships that will be generally applicable to the range of understory and canopy conditions in this, and possibly all, old-growth tropical rain forests.

#### Canopy height: the importance of methods

In the present study we sought to describe the distribution of canopy heights at the scale of 100–1000 ha. We

used random sampling stratified over large landscape units to avoid subjective selection of “good” forest, gaps, or other site types. Three previous studies (Holdridge et al. 1971; Sanford et al. 1986; Lieberman and Lieberman 1994) have also reported measurements on canopy heights at La Selva. Our results differ substantially from all three. The differences among studies illustrate the importance of the methods used and the universe to which one wants to extrapolate.

From measurements in a 0.8-ha plot, Holdridge et al. (1971) reported an average canopy height of 32.5 m for La Selva, a value nearly 50% higher than ours. Part of the difference is likely to be due to our use of landscape-wide random sampling, compared with their “typic” sampling design. There are certainly local areas within a forest where canopy height is higher than the landscape average. Canopy height in our transect 15, for example, averaged 28.5 m. This transect, however, had the highest mean canopy height of the 15 transects. The median height of the canopy of the nonswamp old-growth landscape at La Selva is much lower than 32.5 m.

Lieberman and Lieberman (1994) estimated crown foliage distributions by measuring maximum tree heights and calculating projected crown area along a transect (360 m long) at La Selva. They found that crowns of trees  $\geq 30$  m tall covered only 5.6% of that transect. In contrast, we found 13.3% of the canopy heights at La Selva were  $\geq 30$  m ( $N = 615$ , 15 transects combined). Without further data one can only speculate on the source of this marked difference between the landscape-scale data and findings from a single transect.

Based on interpretation of aerial photographs of La Selva, Sanford et al. (1986) reported that 6.3% of the forest was in gaps, defined as sites with canopy  $< 5$  m high. This is a minimum value, because gaps  $< 40$  m<sup>2</sup> were not detected. In contrast, we found only 2.9% of canopy heights were  $< 5$  m ( $N = 615$ , all transects combined). The area covered by Sanford et al.’s (1986) sample appears to have been in the order of dozens of hectares. Very local variation in canopy height or small-scale siting effects are thus not likely explanations for the observed difference between studies. The aerial photograph interpretations, however, were not ground truthed, nor was evaluation made of repeatability or accuracy. In this case, the possibility that errors of measurement account for the difference in findings cannot be ruled out.

#### Light environments and canopy tree regeneration

All seven species of trees whose sapling microsites were compared with the random background at La Selva have been shown to respond to higher light with increased growth and (or) survivorship (Clark and Clark 1992). It is therefore interesting that the five species of nonpioneers were all found in microsites significantly darker than the random background. One hypothesis to explain this pattern is that all five species established in higher light conditions that have since declined in light availability (light levels can decline rapidly in high-light microsites in the La Selva understory; Rich et al. 1993). Supporting this interpretation are the observed long-term (several year) declines in sapling crown position previously reported for these species (Clark et al. 1993).

Based on this comparison, it is now evident that the small saplings of all of these seven species of canopy trees are distributed nonrandomly with respect to understory light environments at La Selva. To evaluate the generality of the patterns described here will require data on the microsite distributions of other tree species in this and other tropical rain forests. Given the rarity of high-light microsites at seedling levels in closed-canopy old-growth forests, we expect very few of the tree species to have specialized on the high end of this key resource gradient (cf. Denslow 1980). On the other hand, it is intriguing that we found no species whose sapling microsite distributions were either indistinguishable from background or only slightly right-shifted. Similar analyses in other forests will pave the way for quantitatively assessing the relation of plant life histories to available resources.

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