

SPATIAL HETEROGENEITY OF LIGHT AND WOODY SEEDLING REGENERATION IN TROPICAL WET FORESTS

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Abstract. Variation in forest canopy structure influences both understory light availability and its spatial distribution. Because light is a major environmental factor limiting growth and survival of many forest species, its distribution may affect stand-level regeneration patterns. We examined spatial patterning in light availability and seedling regeneration in old-growth, second-growth, and selectively logged stands of tropical moist forest in northeastern Costa Rica. Our objectives were to determine how the frequency distribution and spatial pattern of understory light “microsites” differ among tropical wet forests; whether patterns of seedling regeneration are linked to spatial patterning of light availability; and whether these relationships differ among old-growth, second-growth, and selectively logged forest stands. We used both sensor-based and hemispherical photograph-based methods to measure light availability along three 130–160 m long transects in each of eight stands (three old-growth, three second-growth, and two selectively logged). Woody seedling abundance was assessed at 4 m², 25 m², and full-stand scales (430 m²), and species richness was computed at the 25-m² and full-stand levels. Data were analyzed using both conventional parametric approaches and spatial statistics. Mean light availability did not differ markedly among stand types, but variance and frequency distributions of light availability did. Second-growth stands had significantly higher unweighted canopy openness along solar tracks and a higher frequency of microsites at intermediate light levels. Old-growth stands had greater representation of both low- and high-light microsites, and greater overall variance in light availability. Old-growth stands also had slightly higher abundance and species richness of woody seedlings. Light availability was significantly spatially autocorrelated in all stand types, but patch size (analogous to gap size) was twice as large in old-growth stands, based on sensor data. Seedling abundance was also spatially autocorrelated over greater distances in old-growth than in second-growth stands, often at similar spatial scales to light distribution. The selectively logged stands demonstrated spatial autocorrelation of light and seedling abundance over distances intermediate to the other two stand types. Despite the similarities in patterns of light and seedling distributions, relationships between woody seedling abundance, species richness, and the three light availability measures were not strong or consistently positive, regardless of whether standard regressions or partial Mantel tests were applied. Although seedling abundance is likely to be affected by a wide variety of factors, the similarities in the scales of spatial autocorrelation of light and seedling abundance suggest that current seedling abundance distributions may reflect past patterns of light distribution within the stands. Our results confirm the importance of examining spatial dependence of resource availability in studies of forest dynamics, but they also underscore the limitations of a single period of data collection. Long-term studies as well as experimental manipulations of resource availability are needed to establish causal relationships between resource availability and stand-level patterns of seedling regeneration.

Key words: *autocorrelation; forest dynamics; light distribution; Mantel test; old-growth forest; second-growth forest; seedling abundance; spatial heterogeneity; species richness; tropical rain forest; woody seedling regeneration.*

INTRODUCTION

Understory light availability is both a cause and an effect of forest dynamics. Within and among stands, variation in forest canopy structure and foliage height distribution profoundly influences overall understory

light availability as well as its spatial distribution (e.g., Horn 1971, Aber 1979, Bradshaw and Spies 1992, Bal-docchi and Collineau 1994, Brown and Parker 1994). Because light is a major environmental factor limiting growth and survival of many forest species (Chazdon et al. 1996, Whitmore 1996), the spatial patterns of light availability within forest stands are likely to influence stand-level regeneration patterns of woody species (e.g., Clark and Clark 1992, Clark et al. 1996). The relationship between canopy structure and the spatial distribution of light availability is also likely to

Manuscript received 3 December 1997; revised 13 July 1998; accepted 17 July 1998.

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differ distinctly between old-growth and second-growth stands. Yet, few studies have rigorously examined spatial patterns of light distribution within forests (Clark et al. 1996), or among stands of different successional age (Walter and Himmeler 1996), and even fewer studies have linked microsite variation in light availability to community- and landscape-level patterns of woody regeneration (MacDougall and Kellman 1992, Clark et al. 1996). Such stand-level studies of light conditions are critical for understanding the role of spatially heterogeneous resources in population- and community-level processes.

The work presented here addresses three key questions regarding the relationship between light distribution and forest dynamics: (1) How do tropical wet forests vary in the frequency distribution and spatial pattern of light "microsites" within the understory? (2) Are patterns of seedling regeneration linked to spatial patterning of light availability? and (3) Do these relationships differ among stands with different disturbance histories? To answer these questions we compared stand-level variation in light availability, woody seedling abundance, and woody seedling species richness among eight wet tropical forest stands in the Atlantic lowlands of Costa Rica.

In northeastern Costa Rica, 15–20 yr old second-growth stands are shorter, have more even-aged canopies and exhibit less canopy disturbance compared to old-growth stands (Guariguata et al. 1997). Although basal area does not differ significantly between second-growth and old-growth stands, canopy tree species richness (trees >5 cm dbh) is substantially lower in the second-growth stands (Guariguata et al. 1997). Based on these differences in forest structure and species composition, we predicted greater variability and a larger spatial scale of variation in understory light availability in old-growth stands; that is, old-growth stands should be more "coarse-grained" in terms of the patch structure of light availability, whereas second-growth stands should be more "fine-grained." Because of the greater variation in light conditions expected, we further predicted higher variation in seedling abundance and greater species richness of woody seedlings in the old-growth stands (Ricklefs 1977, Orrians 1982, Denslow 1987). We expected the selectively logged stands to have greater canopy disturbance and therefore increased variation in light availability and woody seedling abundance compared both to old- and second-growth stands. Within and among stands, we predicted a positive relationship among seedling abundance, seedling species richness, and light availability.

Using geostatistics, we examined the spatial scale of light variation and seedling abundance within these stands at distances from 1 to 80 m. We compared our findings based on sensor measurements of light availability with those based on analyses of hemispherical photographs. Finally, we examined relationships between local light availability and local woody seedling regeneration (abundance and species richness), con-

trolling for spatial autocorrelation. In this way, we developed a comparative approach that is both statistically rigorous and ecologically meaningful.

METHODS

Stand selection

The Sarapiquí region of northeastern Costa Rica is a mosaic of active pastureland, small- and large-scale agriculture, second-growth forest, selectively logged forest, and old-growth forest in protected areas (Butterfield 1994). Of the eight stands we selected, four sites were located at the Organization for Tropical Studies' La Selva Biological Station (McDade and Hartshorn 1994); the other four sites were located on private farms within the Sarapiquí region. Land-use history of each stand was determined by a combination of historic records (Pierce 1992), aerial photographs, satellite images, and interviews with local residents and landowners (Table 1). Second-growth stands were cleared for pasture in the early- to mid-1970s, actively managed for 4–6 yr, and subsequently abandoned in the late 1970s or early 1980s. Remnant canopy trees were found in all second-growth stands (Guariguata et al. 1997). In the two selectively logged stands, commercial tree species >70 cm dbh were removed 15–20 yr before study. Vegetation structure, floristics, soils, and soil seed banks of these stands are described elsewhere (Hartshorn and Hammel 1994, Guariguata et al. 1997, Guariguata and Dupuy 1997, Dupuy and Chazdon 1998).

At each site, a series of three, roughly parallel 130–160 m transects were laid out to avoid forest edges and steep slopes. The transects did not traverse any obvious environmental gradients, were located 50 m apart wherever possible, and were never <25 m apart. The same transects were used for sampling light availability, seedling and sapling regeneration, tree species composition and basal area, and the soil seed bank (Guariguata et al. 1997, Chazdon et al. 1998, Dupuy and Chazdon 1998).

Light measurements

Light availability was measured along transects in three different ways: two methods involved sensor measures and one method was based on analysis of hemispherical photographs. Sensor measurements were taken in seven of the eight stands using an LAI-2000 canopy analyzer (LI-COR Incorporated, Lincoln, Nebraska, USA) with a quantum sensor (LI-190SA, LI-COR Incorporated) mounted several centimeters behind the LAI-2000's optical sensor and monitored simultaneously. The canopy analyzer computes leaf area index (LAI) based on a series of five concentric, ring-shaped detectors. Lenses in front of the detector ensure that each ring sensor is exposed to a different portion (zenith angle) of the sky (Welles 1990). Horizontal readings (sensor head held at 0°) were taken at 1-m intervals along the transects at a height of 75 cm using

TABLE 1. Site characteristics of eight forest stands in the Caribbean lowlands of Costa Rica.

Site name (code)	Forest type	Location (latitude; longitude)	Recent land use history	Estimated time since disturbance
Lindero Occidental (LOC)	Second growth	La Selva Biological Station (10°26' N; 84°01' W)	Cleared in 1971–1973. Pasture for 6 yr; regrowth cleared before pasture abandoned	15–17 yr
Peje	Second growth	La Selva Biological Station (10°26' N; 84°02' W)	Cleared in 1972–1974. Pasture for 5 yr; regrowth cleared before pasture abandoned	15–17 yr
La Martita	Second growth	Chilamate (10°27' N; 84°04' W)	Cleared in 1971–1972. Pasture for 4–5 yr, then abandoned	17–20 yr
La Selva	Old growth	La Selva Biological Station (10°25' N; 84°03' W)	No apparent or recorded human disturbance	NA
Chilamate	Old growth	Chilamate (10°27' N; 84°04' W)	No apparent or recorded human disturbance	NA
Cay Rica	Old growth	El Roble (10°26' N; 84°05' W)	No apparent or recorded human disturbance	NA
Intervenido	Selectively logged	La Selva Biological Station (OTS; 10°25' N; 84°02' W)	Logged for >10 yr until the late 1970s. ~3–4 stumps/ha	15–17 yr
Kelady	Selectively logged	Pueblo Nuevo (10°29' N; 84°09' W)	Logged for >10 yr until the early 1980s. ~8–9 stumps/ha	12–14 yr

the full view of the sensor. If a measurement point on the transect was obstructed by a fallen or standing tree, and a measurement could not be taken within 50 cm of the point, the point was considered a missing value. Simultaneous measurements were taken using another set of instruments in a clearing within 1 km of each site using the remote mode on the canopy analyzer unit. Each clearing had an open field of view at least 53° from zenith. The outermost ring sensor of the canopy analyzer (ring five) was masked in all sites to accommodate clearing-size restrictions. Measurements were restricted to periods of uniform, overcast sky in both forest and open sites to avoid direct sun and patchy cloud conditions. Frequent radio communication ensured that no measurements were taken when sun was shining or rain falling in either site. No suitable clearing was available near the Kelady selectively logged stand, so we were not able to use the canopy analyzer or quantum sensors there.

We computed leaf area index (LAI) using LI-COR C2000 software (Welles and Norman 1991). Data from open and transect sites were paired so that measurements were within one (or occasionally two) minutes of one another. Based on the raw values, we were able to eliminate anomalous data (e.g., rain drop or direct sun on one of the sensors). Three sets of computations were made: (1) LAI based on rings one through four (from 0 to 52° of zenith); (2) LAI based on rings one and two (from 0 to 22° of zenith); and (3) LAI based on ring one only (from 0 to 7° of zenith). By masking rings selectively, we could compare relative light availability (based on gap fraction) at specific zenith angles and thus evaluate the size of canopy gaps.

Using the quantum sensors mounted on the canopy analyzers, we also computed percent diffuse light transmittance (PFD forest/PFD open \times 100; PFD, photon

flux density). This technique has been adopted by the Forest Health Monitoring Program (Environmental Protection Agency–U.S. Forest Service) for monitoring transmittance by forest canopies (reviewed in Huston and Isebrands 1995, see also Parent and Messier 1995). Throughout this paper, we refer to percent diffuse light transmittance as %T.

As an indirect measure of light availability, hemispherical photographs were taken in all eight stands. Photographs were taken at 1 m height every 2 m along the transects using a leveled Nikon 8 mm fish-eye lens (180° field of view) mounted on a Nikon 8008 camera body. We used high contrast black and white film (ASA 400, Tri-X, Eastman Kodak, Incorporated, Rochester, New York) and a red, built-in filter to enhance contrast. Photographs were taken within a few weeks to a year of canopy analyzer measurements within each site. Black and white negatives were digitized using a video digitizer (Neotech, Limited, Chandlers Ford, Southampton, UK) and the 256-level gray-scale images were thresholded before analysis. We used an updated version of the program Solarcalc (Chazdon and Field 1987) and a Macintosh to compute weighted canopy openness (WCO) and mean minutes of direct irradiance/day (MDIR). WCO weights openings according to zenith angle (openings directly overhead are most heavily weighted), and is therefore strongly sensitive to canopy openings (gaps) that are directly overhead. In contrast, MDIR integrates the total number of open points along five solar tracks throughout the year and weights each opening equally (Chazdon and Field 1987). Therefore, MDIR is a more sensitive measure of unweighted canopy openness. We also analyzed unweighted canopy openness, based on a subset of 24 photographs from microsites spaced 20 m apart along the transects in second-growth and old-growth stands.

The hemisphere was divided into five evenly spaced zenith angle intervals (0–18°, 19–36°, 37–54°, 55–72°, 73–90°), and the percentage of open points was computed for each interval, incorporating all azimuth angles. This analysis provided a direct assessment of unweighted canopy openness as a function of zenith angle.

Seedling abundance and species richness

Along each transect in all eight stands, woody seedling abundance and species richness were censused in contiguous 1-m² quadrats within 12 mo of the time of light measurements. Seedlings were defined as woody plants between 20 and 100 cm tall. Ramets of clonal species were counted individually if no direct connections were observed. We excluded seedlings below 20 cm height to facilitate reliable identification and to focus our investigation on well-established seedling cohorts. Seedling abundance data were later aggregated for blocks of four contiguous quadrats (quadrat size 4 m²) to avoid large numbers of “empty” quadrats. These data were used to compute semivariogram analyses. To examine variation in seedling abundance and species richness within and among transects, we also used an intermediate spatial scale, the “minitransect.” These 1 × 25 m, spatially independent units were subsampled from the full-length transects and were used to analyze statistical relationships between seedling abundance and light availability (see *Methods: Statistical analysis*). Species accumulation curves for each stand were calculated based on 50 randomizations of quadrat order, using the original data from 1-m² quadrats, as described by Chazdon et al. (1998). A standardized area of 430 1-m² quadrats (the number of 1-m² quadrats available in the site that had the fewest total quadrats [Chilamate]) was used to compare species richness across stands.

Statistical analysis

The distribution of %T, WCO, and MDIR for each stand was first examined using descriptive statistics and plots. Means for the stands were then compared using a nested analysis of variance (ANOVA) model that included terms for stand type (old-growth, second-growth, selectively logged) and site, with replicate sites nested within stand type. Because %T data were available for just one selectively logged stand, the analysis of %T included data from the old- and second-growth sites only. Selectively logged sites were included in the analysis of WCO and MDIR and percentage of open points in each of five zenith angle bands. Both parametric and nonparametric statistics are intrinsically inappropriate for analysis of data that are spatially autocorrelated because the assumption of independence is violated. As the results will show, we found that autocorrelation ceased to be significant at ~20 m; therefore, in addition to analyzing the full data set, data points were subsampled to be 20 m apart (see also Clark et al. 1996). Thus meter 1, 21, 41, and so on were

included in the first model, and the subsampling was repeated 20 times by moving the starting point 1 m further after each sample (2, 22, 42, up to 19, 39, 59 and so on). The same procedure was used to subsample independent data sets from the hemispherical photograph data, but because photographs were taken every 2 m rather than every 1 m, only 10 subsamples were used. The nested ANOVA model was then run on each of the reduced data sets. Results of parametric analyses are included to facilitate presentation of data; however, significance values should be regarded as indicators only.

Both Moran's I autocorrelograms and semivariograms were examined. The analyses yielded the same patterns of results, and we opted to present the majority of results as semivariograms because they provided easily compared values (see below). However, Moran's I autocorrelograms are amenable to statistical tests, and so we tested whether each correlogram demonstrated significant spatial dependence following Bonferroni correction for multiple comparisons (Legendre and Legendre 1983, Legendre and Fortin 1989).

Spatial statistics were computed using GS+ software (Gamma Design Software, Plainwell, Michigan) for LAI data, %T, WCO, MDIR, and seedling abundance in 1 × 4 m quadrats. The LAI data were normally distributed, but %T data were highly skewed and were transformed using the function $\ln(z + 1)$ for all statistical analyses. WCO and MDIR were log-transformed. Seedling abundance was transformed using the function $\ln(z + 1)$. Analyses were performed at the stand level, with data from all three transects included, but relative positions of transects were not specified so that semivariance values were based on within-transect data only.

In a semivariogram, semivariance ($\gamma(h)$) is plotted on the y -axis against lag distance (h) on the x -axis. The lag distance is the step-size used, and the active lag denotes the largest distance considered between points in the semivariance data set, though all data in the data set are included in the analysis. Using GS+ we calculated semivariance and then fit curves to the semivariograms using spherical models as described by Isaacs and Srivastava (1989). For LAI and %T we used a minimum lag distance of 1 m, whereas for indirect light measurements (WCO and MDIR) we used a minimum lag distance of 2 m. We used an active lag of 40 m (except in a few cases where the active lag was increased to improve the fit of the model). The range, nugget, sill, and structural fraction for each analysis were determined from these models (see Rossi et al. 1992). In a spatial analysis of light distribution, the range (the distance along the x -axis at which the semivariogram function stops increasing) is indicative of the patch size of light gaps. Throughout the paper, the word range will be used exclusively in this context. The nugget, the y -intercept of the variogram, is indicative of the percentage of the overall variance not explained by space. The sill, or total sample variance, is

the ordinate value at which the variogram becomes flat. The proportion of total variance explained by spatial dependence is expressed by the structural fraction, which ranges from zero to one (i.e., $(1 - \text{nugget})/\text{sill} = \text{structural fraction}$). The least-squares fit of the spherical model to the semivariance analysis results can be assessed in terms of the model r^2 . A significant r^2 does not, however, ensure significant spatial dependence.

We examined the statistical relationship between light availability and seedling regeneration at three different spatial scales: (1) microsite (4 m²), (2) minitranssect (25 m²), and (3) stand level (430–480 m²). Because %T and seedling abundance data both show significant autocorrelation, statistical assumptions of sample independence are violated (Legendre 1993). We therefore used a partial Mantel test (Mantel 1967) to examine the partial correlation of seedling abundance and mean diffuse transmittance for the microsite scale of 4-m² quadrats, given spatial location. This test controls for spatial autocorrelation in the two variables (Fortin and Gurevitch 1993). We used the method of Smouse et al. (1986) to analyze the three distance matrices, as described by Fortin and Gurevitch (1993). Mantel tests were run using the “R package” (Legendre and Vaudor 1991).

Because very few species are represented within a given quadrat, the microsite scale used to evaluate the partial correlation of seedling abundance with light availability was far too small for evaluating patterns of species richness in relation to light availability. We chose to examine these patterns by dividing the original transects into 11–12 minitranssects for each stand. Each minitranssect was 25 m long and was separated by a 15-m interval from the start of the next minitranssect. In this way, we could subsample the transects for species richness and total abundance at a spatially independent scale with respect to light variation. Differences in seedling abundance and species richness among stands and forest types were assessed using one-way ANOVAs and linear regressions.

Within each minitranssect, mean, median, standard deviation, and coefficient of variation of %T were computed following $\ln(z + 1)$ transformation. We also computed mean WCO and MDIR within each minitranssect. Stepwise multiple regressions were run using these data to examine the dependence of seedling abundance and species richness on the three measures of light availability. These analyses were conducted for each stand individually as well as for the combined set of 82 minitranssects from seven sites (Kelady was excluded because %T data were lacking). Stepwise multiple regressions were done using STATISTICA (StatSoft, Incorporated, Tulsa, Oklahoma); variables were added to the model only if the F statistic for the factor was >1.0 . Thus, significant regression models potentially included one, two, or three factors.

Whole-stand analyses of seedling abundance and species richness in relation to the three measures of light availability were also conducted using stepwise

multiple regressions, as described above. In these analyses, seedling abundance and species richness were standardized to a total of 430 1-m² quadrats, using the mean of 50 randomized species accumulation curves (Chazdon et al. 1998).

RESULTS

Light availability

In all stands, LAI values computed for rings 1–4 were significantly negatively correlated with %T (Pearson correlation, $P < 0.001$). Correlation coefficients ranged from -0.790 (Peje site) to -0.878 (La Selva site). We chose to use %T as our primary measure of light availability and to use the canopy analyzer LAI data as a relative measure of light availability, rather than as a true measure of leaf area index because the LAI values calculated by the LICOR canopy analyzer have not yet been shown to be a precise indicator of actual leaf area index in tropical wet forests (Gower and Norman 1991). This is a conservative approach, as the LAI values of the LAI-2000 have been shown to correlate well with LAI calculated from hemispherical photographs in a temperate oak forest (Wang et al. 1992).

Median %T for the eight sites ranged from 0.98 to 2.0% (Fig. 1a). Mean %T ranged from 1.2 to 2.1% full sun, whereas maximum %T within stands ranged from 4.9% (LOC and Intervenido) to 22.4% (La Selva). Mean %T differed significantly among sites, but not between second- and old-growth stands (Table 2a). The pattern of significance was identical, whether based upon the full data set or independent subsamples. Like %T, WCO differed significantly among sites, but did not differ significantly among stand types (Fig. 1b, Table 2b). In contrast, MDIR varied significantly both among sites and across stand types (Fig. 1c, Table 2c). Second-growth stands had significantly higher MDIR (mean = 184 min/d) than either selectively logged or old-growth stands (mean of 62 and 67 min/d, respectively).

Analysis of minitranssect data (25-m² spatially independent subsamples) showed that standard deviation within minitranssects was significantly dependent on mean %T across stands ($F_{1,80} = 85.465$, $P < 0.001$, $R^2 = 0.517$). Thus, at the 25-m scale, minitranssects with higher mean %T also had greater variance in %T. The coefficient of variation (CV) of %T based on minitranssect data differed significantly among second-growth and old-growth stands (nested ANOVA, $F_{1,4} = 10.686$, $P = 0.0017$), with old-growth stands showing greater mean CV (37.7%) compared to second-growth stands (mean CV = 29.6).

Examination of the frequency distributions of %T reveals that old-growth stands have a greater representation of dark understory microsities than second-growth stands. In old-growth stands, 33–50% of the microsities received $<1\%$ full sun compared to 11–36% of microsities in second growth (Fig. 2a–h; $G = 77.6$,

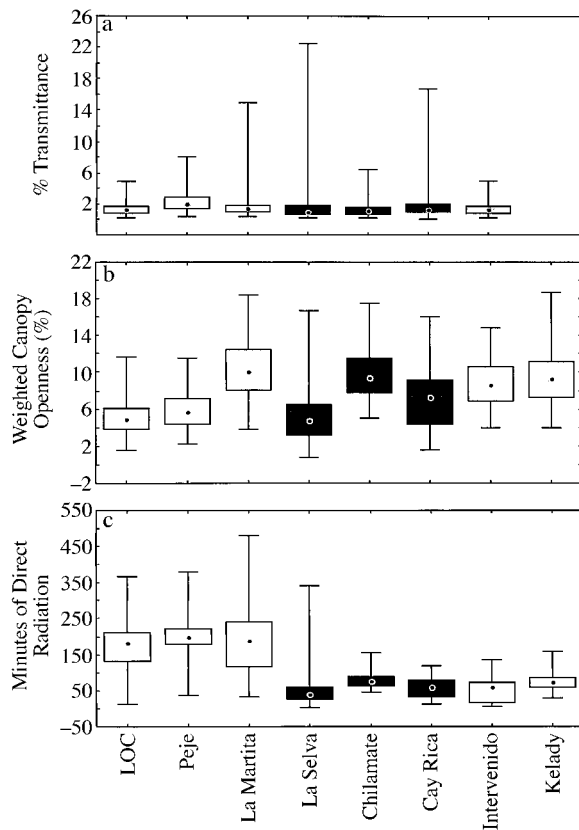


FIG. 1. Box plots showing median (dots), 25th and 75th percentiles (box), and minimum and maximum values (whiskers) for (a) percent diffuse transmittance (%T), (b) weighted canopy openness (WCO), and (c) minutes of direct irradiance/day (MDIR) in three second-growth (unshaded), three old-growth (darkly shaded), and two selectively logged stands (lightly shaded).

$df = 1$, $P < 0.001$). Second-growth stands had twice as many moderately bright understory microsites (between 2 and 5% full sun) as old-growth stands (means of 27.5 and 13.9%, respectively; $G = 62.5$, $df = 1$, $P < 0.001$). In old-growth stands, 6.0% of the microsites had %T values $>5\%$, compared to 2.0% of microsites in second-growth stands (Fig. 2a-h; $G = 32.9$, $df = 1$, $P < 0.001$). The one measured selectively logged stand was similar to old-growth stands in terms of frequency distributions of light microsites (Fig. 2i).

In both second- and old-growth stands, unweighted canopy openness, as determined by analysis of the percentage of open points in five zenith angle bands of the hemispheric photographs, was highest at the zenith and decreased with increasing zenith angle. Old-growth stands have a higher average percentage of open points centered around the zenith ($0-18^\circ$) than do second growth stands (mean ± 1 SE, 18.8 ± 1.7 and $14.7 \pm 1.1\%$ for old- and second-growth stands, respectively), though the stand types did not differ significantly for any zenith angle.

Overall, analysis of mean, median, and frequency

distribution of light microsites using both direct (sensor) and indirect (hemispherical photograph) data suggests that second-growth stands have more numerous, relatively small canopy openings that are more evenly distributed across the canopy compared to old-growth stands, leading to enhanced levels of diffuse light penetration in second-growth stands.

Spatial dependence and semivariogram analysis of light availability

Semivariogram fits based on %T data revealed clear differences in spatial structure between second- and old-growth stands (Table 3a, Fig. 3a). Spherical models provided excellent fits for all stands at lag distances from 1 to 40 m, with R^2 values ranging from 0.84 to 0.99. At this scale, the structural fraction (mean proportion of total variance accounted for by spatial dependence) was 65% for second-growth stands and 74.4% for old-growth stands. Beyond this spatial scale, model fits were generally poor, potentially indicating a random spatial pattern. Second-growth stands had a smaller average range for %T (patch size or scale of spatial dependence, 11.4 m) compared to old-growth stands (22.5 m), indicating that patches of light availability were half the size, on average, in the second-growth stands. At a 40-m spatial scale, the sill (total sample variance) was also lower in the second-growth stands indicating lower overall variance in light availability. The selectively logged site was intermediate in both range (16.3 m) and sill. Moran's I autocorrelograms for all seven sites were significant following Bonferroni correction.

One of the indirect measures of light availability, WCO, also showed excellent fits to spherical semivariogram models (Table 3b, Fig. 3b). For one old-growth site, however, the active lags were increased to up to 50 m to obtain good fits. Two of the second-growth sites showed semivariogram ranges of 13–16 m, similar to the range of %T. The third second-growth site, La Martita, showed a larger range (45.2 m) and a higher structural fraction for WCO than for %T. In this site, hemispherical photographs were taken shortly after a tree fall through one of the transects, and direct-sensor measurements were taken several months later. Semivariogram ranges for WCO averaged 25–29 m for all three forest types and did not show strong differences between stand types. In all sites, the Moran's I autocorrelograms were significant following Bonferroni correction.

MDIR (mean minutes of direct irradiance/day) showed little or no spatial dependence in the second-growth stands or in the Intervenido selectively logged stand; in these sites the model fits were poor at lag distances from 1 to 40 m (Table 3c). In contrast, all three old-growth stands showed excellent spherical model fits. Over 70% of the total variance was accounted for by spatial dependence for these sites, and the range varied from 14.4 m (Chilamate site) to 135 m (La Selva site; Table 3c). For the La Selva old-growth

TABLE 2. Results of nested ANOVA testing for differences among stand types and among sites. ANOVA tables shown are for analyses on the full data set: (a) %T (selectively logged site excluded), (b) weighted canopy openness (WCO), and (c) mean minutes of direct irradiance/day (MDIR).

a) %T				
Source	df	Mean square	<i>P</i>	Significance out of 20 analyses†
Stand type	1	4.88039	0.3407	1
Site	4	4.17905	≤0.0001	12
Error	2760	0.080792		
Total	2765			
b) WCO				
Source	df	Mean square	<i>P</i>	Significance out of 10 analyses‡
Stand type	2	624.533	0.6566	0
Site	5	1363.08	≤0.0001	10
Error	1867	6.66167		
Total	1874			
c) MDIR				
Source	df	Mean square	<i>P</i>	Significance out of 10 analyses‡
Stand type	2	52.6839	0.0077	10
Site	5	3.50909	≤0.0001	10
Error	1864	0.063532		
Total	1871			

† Analysis was conducted 20 times on data subsampled to be spatially independent. Number represents the number of analyses out of 20 that were significant at the 0.05 level. See *Methods: Statistical analysis* for description of subsampling procedure.

‡ Analysis was conducted 10 times on subsampled data to be spatially independent. Number represents the number of analyses out of 10 that were significant at the 0.05 level.

stand, however, the active lag was increased to 90 m to obtain a good fit to the spherical model ($R^2 = 0.79$). The Kelady selectively logged stand showed significant spatial dependence up to 51.2 m. Global significance of the Moran's I autocorrelograms was demonstrated for the three old-growth stands and for both selectively logged stands, but not for the second-growth stands.

Semivariograms of LAI based on rings 1–4 show strikingly similar trends to those for %T (Table 4a; Fig. 3c). For this measure, the proportion of total variance accounted for by spatial dependence averaged 58.7% in the second-growth stands and 62.5% in the old-growth stands. Second-growth stands showed spatial dependence up to 10.7 m, on average, whereas old-growth stands had a mean range of 24.9 m. Again, the selectively logged site was intermediate in both range (20.4 m) and sill. When LAI was computed based on rings 1–2 (from 0 to 22° of zenith), the range of spatial dependence decreased for all stands (Table 4b). When LAI was computed from only the center ring (0 to 7° from zenith), the spatial scale of dependence was even further reduced (Table 4c). These results show that the mean patch size for openings close to the zenith, as indicated by range computed from the center ring only, is 5.7 m in second-growth stands, 16.1 m in old-growth stands, and 12.3 m in the selectively logged stand. This result corroborates the pattern illustrated by the hemispherical photographs: openings surrounding the zenith are substantially smaller in the second-growth stands

than in the old-growth stands. The Moran's I autocorrelograms were significant following Bonferroni correction for all stands and each combination of ring sensors considered.

Woody seedling abundance and species richness

Median seedling abundance in 4-m² quadrats ranged from 5 to 8 seedlings and maximum abundance ranged from 12 seedlings in the La Martita second-growth stand, to 27 seedlings in the Kelady selectively logged stand (Table 5). Mean seedling abundance differed significantly both among stand types (one-way ANOVA, $F_{2,926} = 10.70$, $P < 0.001$) and among sites (one-way ANOVA, $F_{7,921} = 12.216$, $P < 0.001$). Analysis of seedling abundance at the minitranssect level (25 m²) confirmed significant variation among the eight sites (one-way ANOVA, $F_{7,85} = 3.38$, $P = 0.031$) and among stand types (one-way ANOVA, $F_{2,90} = 3.92$, $P = 0.023$, Fig. 4a). At both spatial scales, the stand-type effects reflect lower mean seedling abundance in second-growth stands compared to old-growth stands. Coefficients of variation in seedling abundance ranged from 50.3% (La Martita second-growth stand) to 72.7% (Peje, second-growth stand), with no overall pattern among stand types (Table 5).

In the minitranssects, woody species richness also varied significantly among stands (one-way ANOVA, $F_{7,85} = 4.046$, $P < 0.001$) and was significantly higher in old-growth stands than second-growth stands (one-

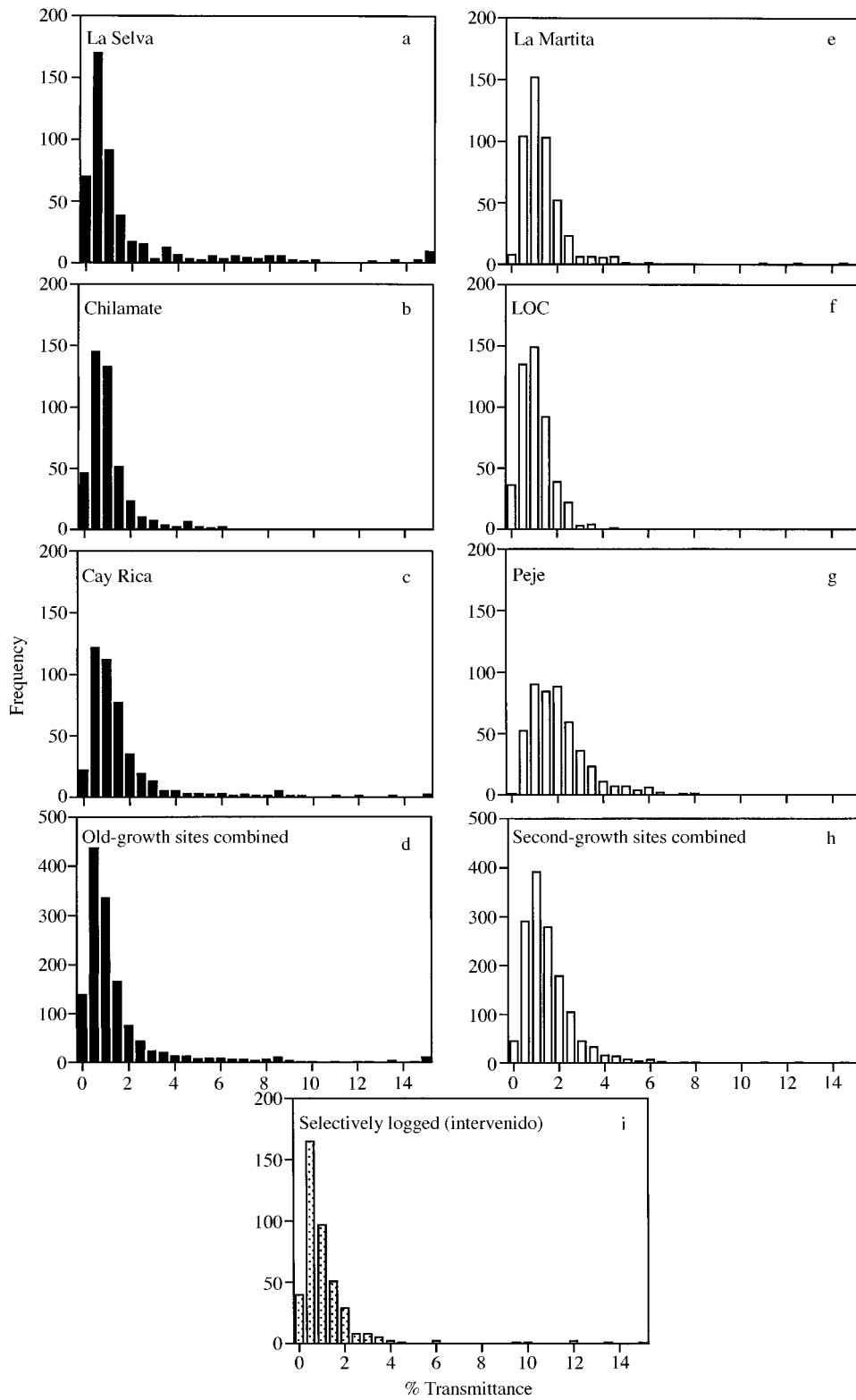


FIG. 2. Frequency distribution histograms of percent diffuse transmittance (%T) in (a–d) old-growth, (e–h) second-growth, and (i) selectively logged stands. Dark bars indicate old-growth stands, open bars indicate second-growth stands, and dotted bars indicate the one selectively logged stand. A standardized number of data points (430, the number of samples in the site with the fewest total samples) was used to facilitate comparison.

TABLE 3. Parameters of semivariogram models.

Site	Nugget	Sill	Structural fraction	Range	R^2
a) %T (active step 1m)					
Second growth					
LOC	0.022	0.055	0.591	12.9	0.848**
Peje	0.019	0.053	0.639	14.3	0.887**
La Martita	0.011	0.038	0.720	6.9	0.841**
Mean	0.017	0.049	0.650	11.4	0.859
Old growth					
La Selva	0.040	0.146	0.728	34.5	0.992**
Cay Rica	0.015	0.087	0.829	17.4	0.972**
Chilamate	0.022	0.069	0.674	15.6	0.928**
Mean	0.026	0.100	0.744	22.5	0.964
Selectively logged					
Intervenido	0.021	0.077	0.735	16.3	0.856**
b) WCO (active step 2m)					
Second growth					
LOC	0.049	0.089	0.449	13.6	0.739**
Peje	0.053	0.102	0.480	16.0	0.938**
La Martita	0.029	0.086	0.657	45.2	0.950**
Mean	0.044	0.092	0.529	24.9	0.867
Old growth					
La Selva	0.092	0.142	0.352	20.5	0.768*
Cay Rica†	0.037	0.151	0.757	49.7	0.985**
Chilamate	0.035	0.082	0.572	11.4	0.883**
Mean	0.055	0.125	0.560	27.2	0.944
Selectively logged					
Intervenido	0.033	0.074	0.551	18.0	0.904**
Kelady	0.050	0.090	0.449	32.3	0.897**
Mean	0.041	0.082	0.500	25.2	0.901
c) MDIR (active step 2m)					
Second-growth					
LOC	0.361	0.397	0.091	84.9	0.069
Peje	0.140	0.165	0.154	89.5	0.156
La Martita	0.217	0.247	0.121	24.7	0.211
Mean	0.239	0.270	0.122	66.4	0.145
Old growth					
La Selva††	0.156	0.586	0.734	135.0	0.971**
Cay Rica	0.054	0.170	0.681	46.2	0.976**
Chilamate	0.042	0.073	0.427	14.4	0.742**
Mean	0.084	0.276	0.614	65.2	0.860
Selectively logged					
Intervenido	0.048	0.059	0.199	24.2	0.411
Kelady†	0.055	0.084	0.346	51.2	0.791**
Mean	0.051	0.072	0.272	37.7	0.509

Notes: Percent diffuse transmittance (%T) data were transformed by the function $\ln(z + 1)$; weighted canopy openness (WCO) and minutes of direct irradiance/day (MDIR) were transformed using the function $\ln(z + 0)$. Parameters listed were estimated from spherical models fit to semivariograms. The active lag is 40 m unless stated otherwise. The nugget indicates the percentage of the overall variance not explained by space. The sill, or total sample variance, is the ordinate value at which the variogram becomes flat. The total fit of the model is expressed by the structural fraction. The range is the distance along the x -axis at which the semivariogram function stops increasing and is indicative of the patch size of light gaps. The least-squares fit of the spherical model to the semivariance analysis results can be assessed in terms of the model R^2 .

* $P < 0.05$; ** $P < 0.01$.

† Active lag set at 50 m.

†† Active lag set at 90 m.

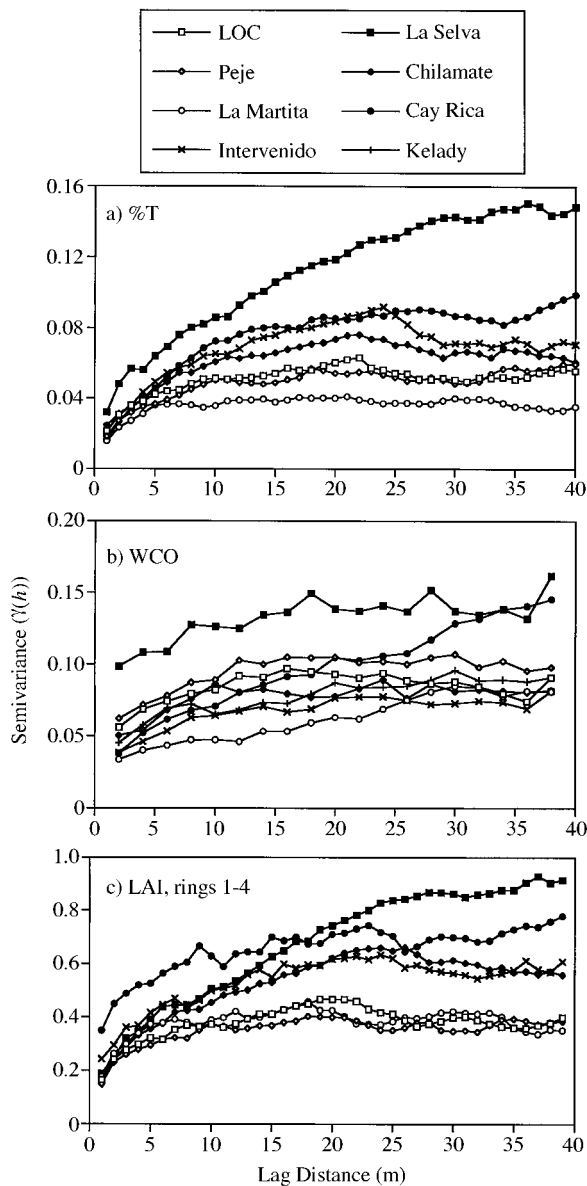


FIG. 3. Semivariograms for three second-growth (open symbols: LOC, Peje and La Martita), three old-growth (closed symbols: La Selva, Chilamate, and Cay Rica), and two selectively logged stands (crossed symbols: Intervenido and Kelady) of (a) percent diffuse transmittance (%T); (b) weighted canopy openness (WCO); and (c) LAI calculated for rings 1-4.

way ANOVA among stand types: $F_{2,90} = 4.488$, $P = 0.014$, Scheffé's post-hoc test, $P = 0.030$). Based on the minitranssect data for all eight stands, species richness was significantly dependent on seedling abundance ($F_{1,91} = 134.29$, $R^2 = 0.596$, $P < 0.001$). When seedling abundance was included as a covariate, species richness did not vary significantly with stand type (one-way ANOVA, $F_{2,89} = 0.831$, $P = 0.439$).

At the stand level, woody seedling species richness varied from 94.2 to 139 species/430 m² (Table 5). As

was the case at the minitranssect level, variation among stands in seedling species richness was significantly dependent upon total seedling abundance ($F_{1,6} = 15.23$, $R^2 = 0.7173$, $P = 0.008$).

Spatial dependence of woody seedling abundance

Semivariance models of woody seedling abundance showed significant fits to the spherical model in six of the eight stands, although fits were not as strong as for light availability (R^2 ranged from 0.48 to 0.86, Table 6, Fig. 5). In two second-growth stands, LOC and Peje, 55 and 66% of the total variance, respectively, was accounted for by spatially dependent variance; seedling abundance showed strong spatial dependence at lag distances of 15 and 8 m (Table 6, Fig. 5a). Two old-growth stands, La Selva and Chilamate, showed strong spatial dependence over lag distances of 14.9 and 91.6 m, with ~50% of the total variance accounted for by spatial dependence (Table 6). The Cay Rica old-growth stand showed a weaker, though still significant fit to the model, and a range of 67.5 m. The two selectively logged sites had intermediate ranges of spatial dependence (13.7 and 14.7 m), but only in the Kelady site was there a significant fit to the spherical model. Semivariograms of seedling abundance for all three old-growth stands show a similar two-phase spatial pattern, with one sill at 12 m and a second sill at 24-28 m (Fig. 5a). This pattern was not observed within the second-growth or logged stands (Fig. 5b).

Moran's I autocorrelograms for seedling abundance were significant following Bonferroni correction for all stands but the La Martita second-growth and Kelady selectively logged stand. The semivariogram for the Kelady stand fit the spherical model well, but the structural fraction was relatively low (45%), potentially explaining the nonsignificant Moran's autocorrelogram. In contrast the selectively logged Intervenido stand had a slightly higher structural fraction (50%) and this may explain why the stand showed significant autocorrelation despite a nonsignificant fit of the semivariogram to the spherical model.

Seedling regeneration in relation to light availability

Microsite scale.—Partial Mantel tests were run on a total of 21 individual transects from seven stands, using mean %T and total seedling abundance in the corresponding 4-m² quadrats. Only four transects showed a significant partial correlation of seedling abundance and light availability (Table 7), and, among these four transects, the direction of the correlation was not consistent. Two transects (Peje 3 and Chilamate 2) showed positive partial correlations, indicating that seedling abundance increased with light availability, whereas two transects (La Selva 3 and La Martita 3) showed negative partial correlations.

Minitranssect scale.—Stepwise multiple regressions of woody seedling abundance on light availability were assessed within each stand using data from the 25-m

TABLE 4. Parameters of semivariogram models based on canopy analyzer data.

Site	Nugget	Sill	Structural fraction	Range	R^2
a) LAI, Rings 1–4					
Second growth					
LOC	0.188	0.405	0.536	13.7	0.741**
Peje	0.158	0.374	0.578	11.7	0.880**
La Martita	0.130	0.369	0.648	6.7	0.730**
Mean	0.159	0.383	0.587	10.7	0.784
Old growth					
La Selva	0.211	0.889	0.763	34.0	0.991**
Cay Rica	0.396	0.707	0.440	18.6	0.875**
Chilamate	0.199	0.607	0.672	22.1	0.946**
Mean	0.269	0.734	0.625	24.9	0.937
Selectively logged					
Intervenido	0.217	0.557	0.610	20.4	0.946**
b) LAI, Rings 1–2					
Second growth					
LOC	1.073	2.132	0.497	7.60	0.813**
Peje	1.025	2.181	0.530	11.70	0.758**
La Martita	0.603	1.838	0.672	6.70	0.610**
Mean	0.900	2.050	0.566	8.70	0.727
Old growth					
La Selva	1.760	4.623	0.619	26.10	0.970**
Cay Rica	1.420	3.594	0.605	19.00	0.938**
Chilamate	1.220	2.250	0.494	13.10	0.814**
Mean	1.467	3.489	0.573	19.40	0.907
Selectively logged					
Intervenido	1.080	3.242	0.667	14.00	0.860**
c) LAI, Ring 1					
Second growth					
LOC	2.150	4.953	0.566	6.00	0.775**
Peje	2.020	6.188	0.674	5.50	0.656**
La Martita	1.820	5.234	0.652	5.50	0.705**
Mean	1.997	5.458	0.631	5.70	0.712
Old growth					
La Selva	3.230	9.770	0.669	16.40	0.936**
Cay Rica	2.790	8.163	0.658	22.20	0.969**
Chilamate	2.420	5.940	0.593	9.80	0.898**
Mean	2.813	7.958	0.640	16.10	0.934
Selectively logged					
Intervenido	2.64	7.400	0.643	12.41	0.608**

Note: For all analyses, the active lag was 40 m, and the active step was 1 m. See Table 3 for description of parameters.

long minitranssects. Multiple regressions were significant for two second-growth stands (LOC and Peje) and two old-growth stands (La Selva and Chilamate), with R^2 ranging from 0.349 (Peje) to 0.711 (La Selva, Table 8a). The contribution of individual independent variables to the regression model was inconsistent across these sites, however. In three stands, only one measure of light availability was sufficiently informative to be included in the regression model; yet this variable was different for each stand. Regression coefficients were negative in many, but not all cases. A forward stepwise multiple regression for all minitranssects (Kelady site excluded) was highly significant ($n = 82$, $F_{2,79} = 9.164$, $P < 0.001$), but only 19% of the variation in seedling

abundance was explained. In this case, both WCO and MDIR had negative regression coefficients (Table 8a).

Similar analyses were conducted using species richness as the dependent variable. Multiple regressions were significant for the three second-growth stands and for one old-growth stand (La Selva), but specific independent variable effects differed among the stands (Table 8b). As with abundance, the combined regression was highly significant, but little of the variation in species richness across minitranssects (14%) was explained by light availability measures. Regression coefficients were also negative for this model (Table 8b).

Stand level.—At the stand level, stepwise multiple regressions of woody seedling abundance on the three

TABLE 5. Woody seedling abundance (number) in 4-m² quadrats and abundance and species richness at the full stand scale.

Site	<i>n</i> †	Seedlings per 4-m ² quadrat (no.)					Full stand	
		Min–Max	Median	Mean	SD	CV (%)	Seedling abundance	Species richness
Second growth								
LOC	120	0–20	6	6.28	4.03	64.2	675.14	128.24
Peje	120	0–21	5	5.67	4.12	72.7	610.54	99.94
La Martita	120	0–12	5	4.88	2.46	50.3	524.62	94.24
Old growth								
La Selva	120	0–20	8	7.81	4.19	53.7	840.28	126.28
Cay Rica	117	0–18	5	6.16	3.91	63.5	526.00	117.22
Chilamate	107	0–14	5	5.43	3.02	55.6	666.60	108
Selectively logged								
Intervenido	112	0–17	5	5.69	3.65	64.3	609.44	119.4
Kelady	113	0–27	8	8.49	4.46	52.6	912.22	139.8

Note: Stand abundance and species richness were computed as the average of 50 randomized orders of 430 pooled 1-m² quadrats.

† Total number of 1 × 4 m quadrats in the stand.

measures of light availability were significant ($n = 7$, $F_{2,4} = 8.774$, $R^2 = 0.814$, $P = 0.034$). Two independent variables were included in this model. WCO was the first variable included, and showed a significantly negative regression coefficient ($P = 0.016$). MDIR also showed a negative regression coefficient, but was not

a significant factor ($P = 0.121$). When stand-level species richness was used as the dependent variable, the multiple regression was even more significant ($n = 7$, $F_{3,3} = 16.991$, $R^2 = 0.944$, $P = 0.022$). In this case, all three light variables were included as factors in the model (WCO, $P = 0.079$; %T, $P = 0.026$; MDIR, $P = 0.031$) and all three had negative regression coefficients. Among all eight stands studied, woody species richness was significantly dependent on seedling abundance ($n = 8$, $F_{1,6} = 15.23$, $R^2 = 0.717$, $P = 0.008$).

Finally, seedling abundance at the stand level was significantly correlated with the semivariogram range of %T (Table 3a). As range (patch size) increased among stands, woody species richness also increased ($n = 7$, $F_{1,5} = 7.272$, $R^2 = 0.77$, $P = 0.043$).

DISCUSSION

Our study had three major objectives: (1) to compare the frequency distribution and spatial pattern of light microsites in old-growth, second-growth, and selectively logged stands of wet tropical forests, (2) to determine whether patterns of seedling regeneration were linked to spatial patterning of light availability, and (3) to determine whether patterns of light and seedling distribution differ among sites with differing disturbance history. The results demonstrated that there is significant spatial patterning of both light availability and seedling distribution, and that the scale of the pattern differs with land-use history. The scale of spatial pattern was often similar for both seedling and light distribution, but despite these similarities, the correspondence between light availability and seedling abundance was weak and inconsistent among stands.

Patterns of light availability

Average light conditions were similar across all three stand types, and we found no consistent differences in median or mean percentage diffuse transmittance (%T) or weighted canopy openness (WCO) between stand

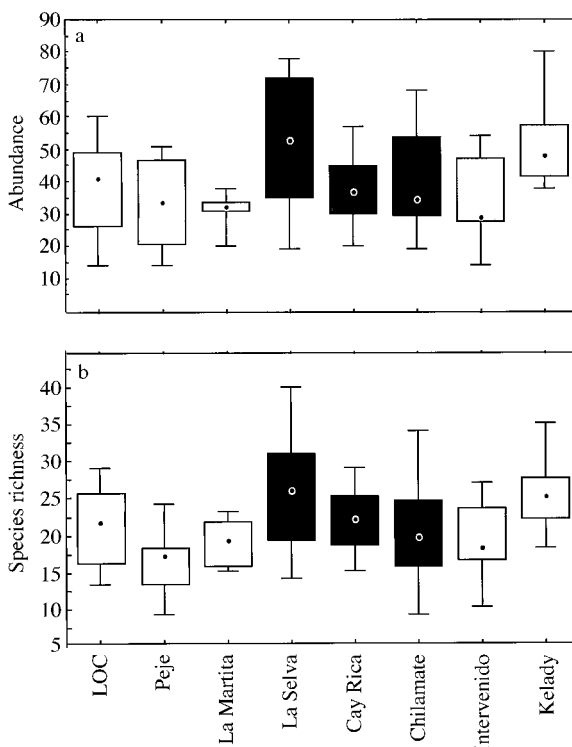


FIG. 4. Box plots for (a) woody seedling abundance and (b) species richness in three second-growth (unshaded), three old-growth (darkly shaded), and two selectively logged stands (lightly shaded) at the minitranssect scale (25 m²). Dots mark median values, the boxes mark 25th and 75th percentiles, and the whiskers mark minimum and maximum values.

TABLE 6. Semivariance statistics for seedling abundance in 4-m² quadrats.

Site	Active lag (m)	n	Nugget	Sill	Structural fraction	Range	R ²
Second growth							
LOC	40	120	0.135	0.300	0.550	15.00	0.829**
Peje	24	120	0.118	0.345	0.658	8.00	0.836*
La Martita	24	120	0.171	0.237	0.278	19.50	0.776
Mean			0.141	0.294	0.495	14.20	0.483
Old growth							
La Selva	80	120	0.178	0.374	0.524	91.60	0.832**
Cay Rica	80	117	0.257	0.390	0.341	67.50	0.535**
Chilamate	40	107	0.125	0.255	0.509	14.90	0.859**
Mean			0.187	0.340	0.458	58.00	0.777
Selectively logged							
Intervenido	44	112	0.175	0.349	0.499	13.70	0.483
Kelady	36	113	0.133	0.242	0.450	14.20	0.856**
Mean			0.154	0.296	0.474	13.95	0.666

Note: Data transformed using $\ln(z + 1)$. All data were fitted to a spherical function. For parameter descriptions see Table 3.

types. This overall similarity may reflect the equivalent tree basal areas in these stands (Guariguata et al. 1997). However, our results confirm our initial prediction that second-growth stands are more homogeneous with regard to variation in light availability compared to old-growth and selectively logged stands. Comparisons of frequency distribution revealed that old-growth stands had more dark understory sites (<2% full sun) and more sites with >5% full sun than second-growth

stands. Likewise, second-growth sites had a greater proportion of understory sites at intermediate light levels (2–5% full sun). Second-growth sites also had significantly greater MDIR, a measure of unweighted canopy openness along solar tracks. Old-growth stands showed significantly higher coefficients of variation in %T compared to second-growth stands. The higher sills of the semivariograms also indicate higher total variance for all three measures of light availability within

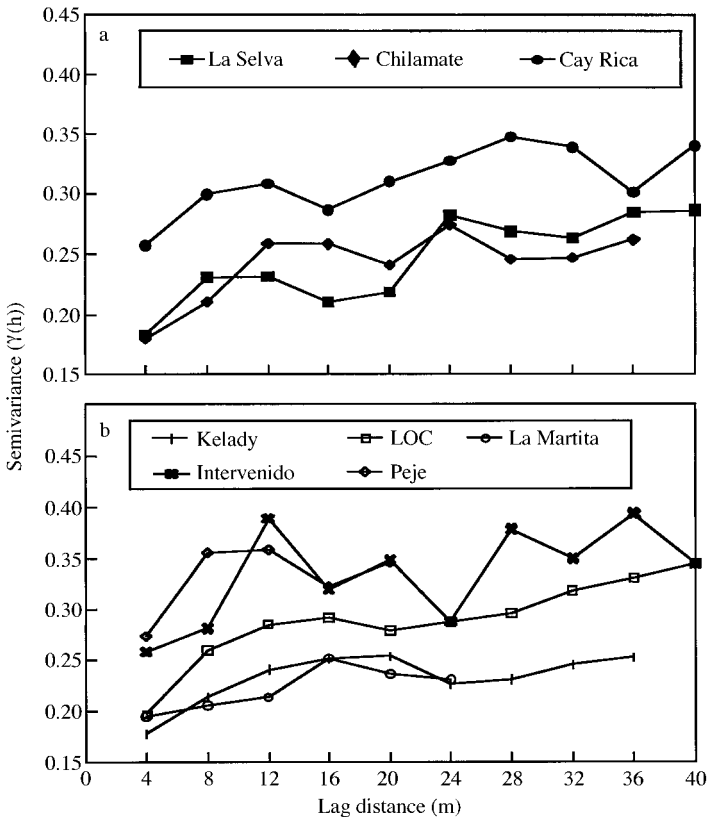


FIG. 5. Seedling abundance semivariograms for (a) three old-growth, and (b) three second-growth stands (LOC, La Martita, and Peje) and two selectively logged stands (Kelady and Intervenido).

TABLE 7. Results of partial Mantel test examining the partial correlation of seedling abundance and diffuse transmittance, keeping effects of spatial location constant.

Site transect	<i>n</i>	<i>r</i> (A.B.C)	<i>P</i>
LOC T1	40	0.083	0.107
LOC T2	40	0.040	0.286
LOC T3	40	-0.008	0.467
Peje T1	40	-0.006	0.492
Peje T2	40	0.006	0.412
Peje T3	40	0.161	0.042
La Martita T1	40	0.030	0.313
La Martita T2	40	0.031	0.271
La Martita T3	40	-0.119	0.029
Intervenido T1	32	-0.012	0.448
Intervenido T2	40	0.032	0.270
Intervenido T3	40	0.015	0.352
La Selva T1	40	-0.011	0.494
La Selva T2	40	0.066	0.219
La Selva T3	40	-0.115	0.052
Cay Rica T1	40	0.105	0.101
Cay Rica T2	37	0.025	0.323
Cay Rica T3	40	-0.072	0.227
Chilamate T1	30	0.027	0.329
Chilamate T2	40	0.349	0.003
Chilamate T3	37	0.019	0.365

Notes: Values in bold are statistically significant at $P < 0.06$. The partial Mantel statistic, $r_{A,B,C}$ is the correlation between matrix A (seedling abundance) and B (diffuse transmittance) given C (spatial location).

old-growth stands compared to the second-growth stands. This combination of lower variation, relatively more frequent understory microsites at intermediate light levels, and high MDIRs suggests that second-growth sites have more, but smaller, canopy openings

than old-growth stands. In the second-growth stands, these frequent, small openings are more evenly distributed across the canopy than in old-growth stands, leading to enhanced diffuse light penetration. In old-growth stands, larger gap size leads to a greater proportion of open points at angles close to the zenith, explaining the greater frequency of microsites receiving >5% full sun. Notably, we predicted that the selectively logged sites would be more variable than second- and old-growth stands, but for most measures they were intermediate to the other two stand types. This pattern suggests that 15–20 years after logging, these sites have largely recovered old-growth canopy structure.

Although these differences in microsite frequency are subtle, they are likely to be important given the generality of light limitation in understory plants, and the linear response of photosynthesis at low PFD (Chazdon et al. 1996). These results demonstrate that effects of forest structure on light distribution may be best revealed by examining frequency distributions rather than by comparing means of light availability (Chazdon and Fetcher 1984, Baldocchi and Collineau 1994, Brown and Parker 1994).

Like many ecological variables, light is not distributed independently among sites (Fortin et al. 1989, Legendre and Fortin 1989, Rossi et al. 1992), and our analysis demonstrated measurable spatial dependence of light availability, the scale of which varied predictably with stand history. For both direct measures of light availability (%T and LAI), and for one of the two

TABLE 8. Results of stepwise multiple regressions of (a) woody seedling abundance and (b) species richness on mean %T, mean WCO, and mean MDIR in 25-m² minitranssects.

Regression	Second growth			Old growth			Selectively logged		
	LOC	Peje	La Martita	La Selva	Chilamate	Cay Rica	Intervenido	Kelady	Combined
a) Woody seedling abundance									
<i>n</i>	12	12	12	12	11	12	11	11	82
<i>R</i> ²	0.393	0.349	0.325	0.711	0.508	NF†	0.139	NF	0.188
<i>P</i>	0.029	0.043	0.170	0.015	0.014	NF	0.259	NF	0.000
Factor									
WCO	0.029 (-)	NI‡	0.289 (-) 2	0.017 (-) 1	NI	NI	NI	NI	0.001 (-) 1
MDIR	NI	0.043 (+)	0.177 (-) 1	0.160 (+) 2	NI	NI	NI	NI	0.018(-) 2
%T	NI	NI	NI	0.125 (-) 3	0.014 (+)	NI	0.259 (+)	no data	NI
b) Species richness									
<i>n</i>	12	12	12	12	11	12	11	11	82
<i>R</i> ²	0.712	0.532	0.368	0.497	0.292	NF	NF	NF	0.144
<i>P</i>	0.015	0.033	0.037	0.010	0.086	NF	NF	NF	0.002
Factor									
WCO	0.059 (-) 2	NI	0.037 (-)	0.010 (-)	NI	NI	NI	NI	0.015 (-) 2
MDIR	0.084 (+) 1	0.033 (+) 1	NI	NI	NI	NI	NI	NI	0.015 (-) 1
%T	0.138 (-) 3	0.095 (+) 2	NI	NI	0.086 (+)	NI	NI	no data	NI

Note: Factors were included in the regression model if $F > 1.0$. For individual factors, *P* levels for regression coefficients are shown, followed by the sign of the partial regression (in parentheses) and order in which variables were added to the model. For Kelady, %T data were not available. The Kelady site was excluded from combined analysis using %T.

† NF, no factors included in multiple regression model with $F > 1.0$.

‡ NI, factor not included in model because $F < 1.0$.

indirect measures of light availability (WCO), semi-variance analysis revealed that the patch size of spatial dependence of light availability (the range) was, on average, 50% smaller in second-growth stands than old-growth stands. Our spatial analyses concur with those of Clark et al. (1996) in demonstrating that spatially independent samples of light availability can be collected at distances of 20 m or more. Becker and Smith (1990) considered six indices of light availability, all calculated from canopy photographs, and for these indices found a similar spatial scale of autocorrelation to what we found. Studies such as these allow us to examine how the scale of spatial dependence of light availability influences the appropriate scale for sampling independent data points to develop spatially explicit models of forest dynamics (Smith and Urban 1988, Weishampel et al. 1992, Pacala et al. 1996).

Because it is generally recognized that a forest canopy is a heterogeneous matrix of different ages of gap recovery (see Lieberman et al. 1989 and citations therein), we can consider the patch size of light availability to be an indication of gap size. The spatial scale of patches of light availability in the La Selva old-growth stand based on %T, LAI, and WCO (20–35 m) approximates the range of canopy gap sizes (mean gap area of 161 m²) in old-growth forest at La Selva, as determined by Sanford et al. (1986). Differences in average patch size between second-growth and old-growth stands, therefore, probably reflect differences in gap sizes. However, these data should not be interpreted as suggesting that gaps are regularly distributed in old-growth forests. For such an interpretation, periodicity in the spatial autocorrelograms would be needed (Breshears et al. 1997). We did find some negative autocorrelation in old-growth (but not second-growth) stands over lag distances of 80 m (data not shown), as did Clark et al. (1996). Becker and Smith (1990) found a weak trend toward periodicity in autocorrelograms for tropical forests in Panama during an El Niño year; however, they suggested that this pattern might result from regularly distributed deciduous trees, rather than from regularity of gap distribution.

Differences in spatial scale of light heterogeneity could be due, in part, to differences in tree allometry and understory vegetation among the stand types. Based on measurements of a stratified subsample of trees (>10 cm dbh) within each of the stands, canopy trees in the second-growth stands have narrower crowns and are taller than in the old-growth stands (one-way ANOVA, $P = 0.003$; R. A. Montgomery and R. L. Chazdon, *personal communication*), permitting increased light penetration between tree crowns. Species-specific differences in canopy tree architecture can also influence patterns of understory light availability within these stands (Kabakoff and Chazdon 1996). Detailed vegetation studies across the same transects discussed here indicate that as the abundance of subcanopy or understory trees and shrubs (<5 cm dbh) in-

creases, light availability at 0.75 m decreases (R. A. Montgomery and R. L. Chazdon, *personal communication*). Thus, dense vegetation in all stand types is likely to minimize the amount of direct light reaching seedling levels, making the distribution of large gaps around the zenith likely to be a critical difference between stand types.

It is not surprising that the shorter, even-aged, more homogeneous canopies of young, second-growth stands would have smaller gap size and a more even distribution of openings across the canopy. On Barro Colorado Island, Panama, large treefall gaps are more frequent in old-growth forest than in second-growth forest (Brokaw 1982), and treefall gaps become more common in second-growth forest with increasing age (Yavitt et al. 1995). Both increased crown size and proximity to existing gaps are associated with larger gap sizes in late secondary and old-growth tropical forests (Hubbell and Foster 1986, Martínez-Ramos and Soto-Castro 1993). Bradshaw and Spies (1992) found a general correlation between stand age and gap-structure development in coniferous forest stands, despite considerable variation within age classes. Linking forest structure with patterns of spatial distribution of light availability will be challenging until we fully understand the relationship between gap recovery, canopy structure, the distribution of foliage in subcanopy and understory layers, and light transmittance (Baldocchi and Collineau 1994, Clark et al. 1996). Despite these inherent difficulties in linking forest structure to light availability, our data do suggest underlying spatial patterns. These results suggest that spatial dependence of light availability may be a good indicator of gap structure in stands with different disturbance histories or of different successional stages.

Light measures compared

Both sensor-based and hemispherical photograph measures of light availability were effective in revealing differences in availability and spatial distribution of light. Of the two indirect measures of light availability, MDIR appears to be a better estimate of diffuse light penetration (and perhaps overall light availability) than WCO. Mean MDIR computed for spatially independent minitranssects (25 m²) was positively correlated with mean %T across seven stands ($R = 0.279$, $P < 0.011$, $n = 82$), whereas mean WCO showed no significant correlation with mean %T ($R = -0.4559$, $P = 0.684$, $n = 82$). In old-growth stands, mean WCO was positively correlated with mean MDIR across minitranssects ($R = 0.648$, $P < 0.000$), but these two measures were not correlated in the second-growth or logged stands ($P = 0.523$ and 0.763 , respectively). Because WCO is strongly weighted by zenith angle, these results indicate that canopy openings are distributed predominantly around the zenith in old-growth stands compared to the other stand types.

Although both direct and indirect measures of light

availability demonstrated spatial dependence, the direct measures showed greater consistency among themselves than the indirect measures. MDIR, though sensitive to differences in diffuse light between stand types, did not reveal patterns of spatial dependence in light availability. The variation between indirect measures most likely arises because all openings across the solar tracks are weighted equally in calculation of MDIR, whereas for WCO open points around the zenith are weighted more heavily. Because MDIR is computed based on five solar tracks, it would only show significant spatial autocorrelation if canopy openings along solar tracks were relatively continuous, leading to large-scale patterning of sunflecks.

Canopy photographs do not predict actual photon flux density reliably or accurately in closed-canopy sites (Whitmore 1993), but they do reveal important features of canopy structure and distribution of openings (Chazdon and Field 1987, Rich 1990). Canopy photographs also enable relative predictions of light availability at different times of year. Analysis of canopy photographs is, however, quite time consuming. Our results demonstrated that the LAI-2000 plant canopy analyzer provides reliable data and direct light measures. The instrument was sufficiently sensitive to distinguish clearly between closed-canopy microsites. Nevertheless, working with the canopy analyzer was logistically demanding at times, due primarily to difficulty in finding nearby clearings of sufficient size, and frequent, unpredictable variation in weather conditions between open and forested sites. The question of whether or not the canopy analyzer accurately predicts the leaf area index of a natural forest stand remains to be addressed (Gower and Norman 1991). Notably, %T can be calculated using just data loggers and quantum sensors. The direct sensor measurements under overcast skies approach (the "SOS method") also has advantages as a standardized instantaneous measure of light availability in that data can be collected in light rain. Our study shows that using different measures of light availability yielded insights that a single measure could not provide; sensor and hemispherical photograph measures of light availability are best viewed as complementary rather than as unique alternatives. Where the focus of a study includes predicting patterns of light availability during the course of a year, or examining canopy structure and the distribution of canopy openings, hemispherical photographs may be preferable. In contrast, if one's objective is to obtain standardized, repeatable measures that are sensitive to subtle variation in understory microsites, a quantum sensor approach is recommended.

Seedling abundance, richness, and spatial distribution

We predicted that woody seedling species richness and abundance would be greater in old- than second-growth forests because of greater heterogeneity of light

distribution (Ricklefs 1977, Orians 1982, Denslow 1987) among other things. At both the 4-m² scale and the 25-m² minitransect scale, second-growth stands showed significantly lower seedling abundance than old-growth stands. As predicted, woody seedling species richness was also lower in second-growth stands. Although we found greater variance in light availability in the old-growth stands, there was no statistical relationship between species richness or seedling abundance and cv of %T. Likewise, though the spatial scale of seedling distribution was generally greater in old-growth than second-growth stands, we did not find a consistent direct relationship between light availability and woody seedling abundance or species richness. We did, however, find a significant positive correlation between woody species seedling abundance and the scale of spatial dependence of light availability across stands.

Our results show that woody seedling species richness is strongly dependent upon seedling density both within and among stands. The pattern of higher seedling species richness and correspondingly higher seedling abundance in the old-growth stands is not surprising, given the higher species richness of trees and greater accessibility to seeds in the old-growth stands. Other studies have shown similar strong relationships between species richness and density for woody species in tropical forests (Denslow 1995, Condit et al. 1996; J. M. Dupuy and R. L. Chazdon, *unpublished data*). Comparative analyses of species richness, therefore, must control for density effects as well as for area effects (Chazdon et al. 1998). In the present study density effects were accounted for by including seedling abundance as a covariate in our analyses of species richness. A prior statistical analysis of woody seedling abundance in these second- and old-growth stands did not find a significant difference between stand types in seedling species richness (Guariguata et al. 1997). The discrepancy between these two analyses arises because the prior analysis was based only on a stand-level comparison (three stands nested within each forest type) and was less sensitive to the relatively small differences between stand types.

Both within and across stands, seedling abundance generally tended to be a weak, and more often than not, a negative function of mean light availability. In a riparian forest of Belize, MacDougall and Kellman (1992) found no correlation between total seedling density and understory light intensity (but see Clark et al. 1996). Of course, differences in woody seedling abundance and species richness are likely to be influenced by a complex set of interacting ecological factors that may act at the microsite, minitransect, or stand level. In addition to light availability, these include (1) propagule dispersal (e.g., Howe 1990), (2) competition with monocotyledonous herbs, ferns, and vines (Dirzo et al. 1992), (3) effects of litter depth and soil disturbance (Putz 1983, Molofsky and Augspurger 1992, Vázquez-Yanes and Orozco-Segovia 1992), (4) herbivory

(DeSteven and Putz 1984, Schupp 1988), (5) pathogens (e.g., Augspurger 1984), and (6) effects of drought or nutrient limitation (Burslem et al. 1996, Mulkey and Wright 1996). This complexity means that the amount of variation directly attributable to a single factor (i.e., light) is likely to be low. Nonetheless, because light limits growth and strongly influences seedling survival (Augspurger 1983, Chazdon et al. 1996, Whitmore 1996), we expected to find a positive relationship between light availability and seedling abundance.

Not all of the factors that influence seedling abundance and species richness will lead to a spatially clumped distribution of seedlings. On Barro Colorado Island, leaf litter distribution was not spatially autocorrelated at scales of 1–20 m (Molofsky and Augspurger 1992). Herbivory may be concentrated in patches of high seed/seedling density or in patches of high light availability (Janzen 1970, Clark and Clark 1984, Howe 1990). Light, however, is strongly spatially autocorrelated in these stands, and therefore we can expect that seedling growth and survival responses to light will result in spatial structuring of recruits. The similarity between the scale of autocorrelation of seedling abundance and that of light availability in both second- and old-growth stands suggests a strong influence of light distribution on seedling establishment and supports the view that all else being equal, stands with high spatial dependence of light availability, and larger ranges, should have higher seedling abundance and species richness.

The negative correlation demonstrated in the present study may be explained if *current* seedling patches reflect *former* patches of increased light availability that have since grown dense and deeply shaded (e.g., Smith et al. 1992). Forest understory light conditions are dynamic in both space and time such that the precise spatial location of gaps may change, even though the scale of spatial patterning of light availability remains fairly constant. What effect does this “moving window” of light availability have on spatial patterns of seedling regeneration? If seedlings germinate and establish in gaps, which then rapidly close over at the understory and subcanopy levels, then by the time they grow to be 20–100 cm tall, the seedlings are likely to be found in relatively darker microsites. Seedlings of many rain forest species are capable of surviving without growth for long periods of time, until they are “released” by increased light availability (e.g., Clark 1994). In fact, Clark et al. (1996) found that saplings (1–3 m tall) of five canopy tree species were distributed in significantly darker than random microsites in La Selva old-growth forests and explained these microsites as “black holes” left after former gaps had closed. If these hypotheses hold, then recently germinated seedlings (i.e., seedlings smaller than those we examined) should be more abundant in brighter than average microsites (e.g., Augspurger 1983), and the relationship between light availability and seedling abun-

dance should be nonlinear, an inverse parabola perhaps. Of course, for individual species, the shape of this relationship can be expected to differ (see Clark 1994). Thus, the variability in the relationship between light availability and seedling abundance may in part reflect different species responses, and different times since last gap formation.

To determine the causal relationship between light availability and seedling regeneration, long-term studies are needed. The present study was limited to a single period of data collection. Time lags in data collection resulted from the size of the project and introduced a source of variability into our results. In addition, by considering woody plants between 20 and 100 cm as seedlings, we incorporated variability due to different ages and histories of the seedlings. To expand on the present study, long-term monitoring of light availability (as well as other potentially limiting resources) and the variation therein is needed to determine how spatial dependence varies over time. Combining long-term monitoring with experimental manipulation provides the best method for revealing the interactions among ecological processes that ultimately influence seedling regeneration at the stand level. For example, experimental manipulation of resource availability can be used to measure natural regeneration responses (e.g., J. M. Dupuy and R. L. Chazdon, *unpublished results*), and studies of responses of transplanted seedlings can be used to assess impacts of gap formation (e.g., S. V. B. Iriarte and R. L. Chazdon, *unpublished results*). Finally, surveys of the natural distribution of seedlings with respect to light availability, in conjunction with long-term monitoring of species- or life-history-specific seedling responses to natural variation in light may indicate whether the nonlinear relationship between seedling distribution and light availability proposed herein actually occurs.

Studies of resource distribution in forested ecosystems need to consider not only the average levels, but the variance, frequency, and spatial distributions of these resources (e.g., Fortin et al. 1989, Kelly and Canham 1992, Molofsky and Augspurger 1992, Robertson et al. 1993). The methods applied here allowed us to describe and contrast forest types with regard to spatial distributions of light. While such approaches have been discussed and recommended by others (Clark et al. 1996, Walter and Himmler 1996, Walter and Torquebiau 1997), this study provides the first application of such methods contrasting forests of different ages and land-use histories. Our results clearly demonstrate that similarities in average conditions among forests can obscure biologically important environmental variability, and that an understanding of spatial patterning of resource availability may lead to a better understanding of regeneration processes in tropical wet forests.

ACKNOWLEDGMENTS

We thank Julie Denslow for her critical role in overall project design and development and Manuel Guariguata, Juan

Dupuy, Carolina Gonzalez, and Orlando Vargas for data collection in the field. Marcos Molina and Jeanette Paniagua provided excellent assistance in vegetation sampling, light measurements, and canopy photography. Ann Geissinger and Christopher Bird spent many hours carefully analyzing hemispherical photographs. Debra Klepeis conducted the hemispherical photograph analysis of unweighted openness. We are grateful to Rebecca Montgomery, Marie Jose-Fortin, and Jessica Gurevitch for advice on spatial statistics. Discussions with David and Deborah Clark and Rebecca Montgomery contributed greatly to all phases of this research and analysis. Two anonymous reviewers provided insightful comments on an earlier draft of the manuscript. Finally, we thank the staff of the Organization for Tropical Studies at Duke, Costa Rican Office, and La Selva for their invaluable logistic support. We thankfully dedicate this manuscript to Donald E. Stone, former Executive Director of the Organization for Tropical Studies, whose vision made this research possible. This research was supported by NSF grant DEB-9208031.

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