

FOREST STRUCTURE, CANOPY ARCHITECTURE, AND LIGHT TRANSMITTANCE IN TROPICAL WET FORESTS

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Abstract. Identifying factors that influence variation in light availability within forested ecosystems represents an important component in our understanding of the complex determinants of tree seedling regeneration. We assessed the influence of forest structure and canopy tree architecture on spatial heterogeneity of understory light availability in three old-growth and three second-growth forests in lowland Costa Rica. Forest structure and understory light availability were measured within forest types using contiguous 10 × 10 m quadrats along three 130–160 m transects in each stand. Two 20 × 60 m plots in each forest type were sampled more intensively, including vertical profiles of light availability from 1 to 9 m height. Mean diffuse light transmittance increased from 2% at 1 m height to over 10% at 9 m height and did not differ significantly between forest types at any height. However, the relationships among height classes differed between forest types. Second-growth plots showed a negative spatial autocorrelation for light measurements separated by vertical distances over 4 m. Differences in the vertical distribution of light and foliage suggest that old-growth and second-growth stands differ in vertical organization of the vegetation. The most pronounced structural differences between forest types were found in trees between 10 and 25 cm in diameter at breast height (dbh). In second-growth stands, trees in the 10–25 cm dbh size class were more abundant and differed in allometry. They were taller for a given stem diameter and had narrower crowns for a given height than old-growth trees. Within forest types, we did not find strong relationships between measures of forest structure and light availability, although the strength of these relationships differed between forest types. In both old- and second-growth forest, understory light availability at 0.75 m decreased with increased sapling and shrub density, but was not significantly influenced by local tree density or basal area. From 1-m to 9-m heights, tree density was a significant, but weak, predictor of light availability in old-growth plots. In second-growth plots, tree density showed little or no influence on light availability at heights below 9 m. Our findings challenge the view that, within a forest, canopy and subcanopy vegetation directly influence light transmittance near the forest floor. Instead, we argue that spatial patterning of the light environment occurs through complex interactions among canopy, subcanopy, and understory vegetation.

Key words: *canopy-tree architecture; Costa Rica; crown size; forest dynamics; forest structure; forest succession; light availability; old-growth vs. second-growth tropical rain forests; stand structure and light transmission; tropical rain forest.*

INTRODUCTION

Within forest stands, variation in vegetation composition, structure, and foliage distribution creates spatial variation in light transmittance in the understory, affecting growth and mortality of tree seedlings and saplings. In both temperate and tropical forests, studies of variation in the understory light environment and its effect on tree regeneration have focused on the pervasive effects of canopy vegetation and canopy gaps (Hartshorn 1978, Denslow 1980, Brokaw 1982a, Augspurger 1984, Chazdon and Fetcher 1984, Hubbell and Foster 1986, Martinez-Ramos et al. 1989, Smith et al. 1992, Cornelissen et al. 1994, Sipe and Bazzaz 1995). Yet canopy gaps are ephemeral phenomena, and gap

microsites account for only a small proportion of forested areas at any given time (Clark et al. 1996, Connell et al. 1997, Nicotra et al. 1999). Within forest ecosystems nearly 75% of the area can be classified as “non-gap” or “subcanopy gap” (sensu Connell et al. 1997). Thus, non-gaps represent the most common microsites occupied by canopy-tree seedlings, saplings, and subcanopy trees (Clark and Clark 1992, Lieberman et al. 1995, Clark et al. 1996, Connell et al. 1997).

The strict dichotomy between gaps and closed-canopy sites oversimplifies the complex three-dimensional structure beneath the forest canopy (Pompa et al. 1988, Grubb 1996, Parker and Brown 2000) and emphasizes direct effects of canopy structure on light transmittance in the understory (Lieberman et al. 1989, Lieberman and Lieberman 1991, De Steven 1994, Jones and Sharitz 1998). Yet several studies have shown that subcanopy trees, saplings, palms, ferns, shrubs, and herbs can have a major influence on light availability and tree-

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seedling regeneration within the understory (Denslow et al. 1991, Russell et al. 1998, George and Bazzaz 1999). Moreover, canopy species composition can significantly influence light transmittance within and among stands, in the absence of canopy gaps (Messier and Bellefleur 1988, Canham et al. 1994, Kabakoff and Chazdon 1996).

We examined the influence of forest vegetation composition and structure on spatial variation in diffuse light transmittance in the understory of three mature and three second-growth tropical rain forest stands in the Caribbean lowlands of Costa Rica. To our knowledge, this is the first study to describe detailed relationships between ground-based measures of vegetation structure and within-stand variation in light transmittance in both second-growth and old-growth tropical wet forests. Recent studies in these stands demonstrated striking differences in species composition of canopy and subcanopy woody vegetation, with second-growth stands showing increased dominance by fewer species in the canopy and decreased abundance of subcanopy palms (Guariguata et al. 1997). These second-growth stands also showed lower overall spatial heterogeneity and smaller patch sizes of diffuse light transmittance in understory microsites (Nicotra et al. 1999). Can differences in forest structure and species composition explain these distinct patterns of light heterogeneity? Although theoretical studies propose strong links between canopy architecture, forest structure, and light transmittance (Anderson 1966, Horn 1971, Campbell and Norman 1989, Kuuluvainen and Pukkala 1989), patterns of understory light availability do not always show a clear dependence on forest structure (Ross et al. 1986, Gleeson and Tilman 1990, Brown and Parker 1994, Denslow and Guzman 2000).

In this paper we begin by describing differences between old-growth and second-growth forests in understory light availability, tree architecture, and measures of forest structure such as basal area and density of trees. We then examine relationships between forest structure and understory light availability among quadrats within each forest type. Finally, we compare these relationships between the two forest types. We consider both the horizontal and vertical dimensions of spatial variation in light transmittance and address the following three questions: (1) Can ground-based measures such as tree basal area and stem density predict light availability at different heights within the understory? (2) What are the relative contributions of canopy, subcanopy, and understory woody vegetation to observed variation in understory light availability? (3) Do patterns of understory light transmittance reflect differences in canopy architecture or allometry of dominant tree species?

METHODS

Site selection and history

The study was conducted in the Sarapiquí region of northeastern Costa Rica. This area is classified in the

Holdridge life-zone system as tropical wet forest and receives >4000 mm of rain each year (McDade et al. 1994). The region is a mosaic of agricultural lands, tree plantations, and second-growth, selectively logged, and old-growth forests (Read et al., *in press*). We studied six stands, three in second-growth and three in old-growth forest (Table 1). Three stands were located within La Selva Biological Station (owned and operated by the Organization for Tropical Studies) and three were on private farms. Second-growth stands were cleared for pasture in the early 1970s, grazed for 4–6 yr, and then abandoned. Old-growth stands showed no evidence of human disturbance over the past 200 yr (Denslow and Hartshorn 1994). Stands differed in their degree of isolation from large tracts of forest. These stands were part of a larger study examining how environmental heterogeneity influences the nature and diversity of woody regeneration during tropical rain forest succession in northeastern Costa Rica (Kabakoff and Chazdon 1996, Guariguata et al. 1997, Dupuy and Chazdon 1998, Chazdon and Coe 1999, Nicotra et al. 1999).

Vegetation sampling

We established three parallel 130–160 m transects spaced ~50 m apart in each stand, on level ground. Basal area and density of woody stems ≥ 5 cm in diameter at breast height (dbh) were measured in contiguous 10×10 m quadrats along each transect (13–16 quadrats per transect). Woody shrub and sapling density (≥ 1 m tall < 5 cm dbh) was measured in contiguous 5×5 m plots located in the center of the 10×10 m quadrats (32 quadrats per transect; for detailed methods see Guariguata et al. [1997]). In addition, we established four 20×60 m plots, two in one of the old-growth stands (La Selva) and two in one of the second-growth stands (Lindero Occidental; Table 1). These 20×60 m plots were subdivided into twelve 10×10 m quadrats. In each quadrat, basal area and density were sampled for all woody stems ≥ 5 cm dbh. We also counted all woody and nonwoody stems ≥ 1 m tall but < 5 cm dbh.

Tree architecture and allometry

In three of the 10×10 m quadrats per transect (12 per site), we measured maximum tree height, height to first branching, and crown diameter for trees ≥ 5 cm dbh. In the plots, tree height and crown diameter were measured for all trees ≥ 10 cm dbh. We used a telescoping pole for height measurements below 12 m. For taller trees, we employed the angle-measure method to estimate tree height (Korning and Thomsen 1994). This method has been recommended in tropical wet forest systems to avoid difficulties associated with measurement of horizontal distance in dense vegetation and obscuration of crowns by neighboring trees. We made two measurements of crown diameter, one at the widest point and the other perpendicular to first measurement.

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

Forest type and site	Location (latitude; longitude)	Recent land-use history	Estimated time since disturbance (yr)†
Second-growth			
Lindero Occidental	La Selva Biological Station (10°26' N; 84°01' W)	cleared in 1971–1973; pasture for 6 years; regrowth cleared before pasture abandoned	15–17
Peje	La Selva Biological Station (10°26' N; 84°02' W)	cleared in 1972–1974; pasture for 5 years; regrowth cleared before pasture abandoned	15–17
La Martita	Chilamate (10°27' N; 84°04' W)	cleared in 1971–1972; pasture for 4–5 years, then abandoned	17–20
Old-growth			
La Selva	La Selva Biological Station (10°25' N; 84°03' W)	no apparent or recorded human disturbance	n.a.
Chilamate	Chilamate (10°27' N; 84°04' W)	no apparent or recorded human disturbance	n.a.
Cay Rica	El Roble (10°26' N; 84°05' W)	no apparent or recorded human disturbance	n.a.

† n.a. = not applicable.

For each tree's crown we calculated both area and volume. Crown area was approximated as an ellipse using the two perpendicular measures of crown diameter. Crown volume was estimated as an elliptical cylinder by multiplying crown area by depth. This method overestimates actual crown volume but is a potentially informative estimate of the amount of vegetation in the forest canopy (Terborgh and Petren 1991).

Vertical profile of vegetation

Another measure of vertical structure and stratification of the canopy is the foliage height profile (MacArthur and Horn 1969, Terborgh and Petren 1991). Every 2 m along each transect (80 per transect) the presence/absence of foliage was determined within intervals between 0–1 m and 1–2 m above the forest floor. In addition, every 6 m along each transect (26 per transect) presence/absence of foliage was recorded in the following intervals (0–1, 1–2, 2–5, and 5–10 m) using a telescoping pole. We recorded presence of vegetation if leaves touched the telescoping pole in the interval of interest. Presence of vegetation above 10 m was assessed using a telephoto lens mounted on a tripod located next to the telescoping pole. Intervals (10–15, 15–20, 20–30, and 30–40 m) were sighted through the lens, looking directly above the top of the pole (height = 10 m). If foliage could be focused within an interval, presence was recorded. This method is similar to that used by Welden et al. (1991), but differs in that our method evaluated foliage presence in intervals throughout the vertical transect and did not simply assess maximum vertical foliage height.

Light availability

We assessed forest light environments by measuring percentage transmittance of diffuse photosynthetic

photon flux density (PFD) under overcast sky conditions in the center of each 10 × 10 m quadrat. We measured instantaneous below canopy PFD at 0.75 m height in 1-m intervals along transects using a LI-190 quantum sensor (LI-COR, Lincoln, Nebraska). For this study, we averaged the three center readings from meters 4, 5, and 6 within each quadrat. In plots, PFD was measured along a vertical profile at a single point in the center of each 10 × 10 m quadrat at heights of 1, 2.1, 4.2, 6.5, and 9 m above the forest floor. The quantum sensor was mounted on a small, self-leveling platform atop a telescoping pole.

During all light measurements, above-canopy PFD was measured simultaneously in a nearby clearing using a quantum sensor mounted on a tripod. The sensor was connected to a LI-2000 datalogger that recorded PFD every 15 s (LI-COR). Below-canopy readings were paired with the closest-in-time above-canopy measurements to calculate percentage diffuse transmittance (% transmittance = [below-canopy PFD/above-canopy PFD] × 100). All diffuse PFD measurements were made under overcast sky conditions, avoiding confounding effects of sun flecks and solar angle. This instantaneous measure of percentage diffuse transmittance has been shown to provide a sensitive measure of light availability in understory microsites (Messier and Puttonen 1995, Parent and Messier 1996, Nicotra et al. 1999). Due to nonnormal distribution of light, in statistical analyses we used an inverse log transformation to compute optical density, a metric inversely related to percentage diffuse transmittance.

Statistical analysis

Spatial structure within ecological data presents problems for traditional statistical analysis because

TABLE 2. Moran's *I* coefficient of spatial autocorrelation in stem density of two woody size classes at six sites in northeastern Costa Rica.

Lag distance (m)	Lindero Occidental	Peje	La Martita	La Selva	Chilamate	Cay Rica
Stem density, 10–25 cm dbh						
10 (45)	0.077	0.253	–0.018	–0.109	0.163	0.165
20 (42)	–0.088	0.428*	–0.004	–0.050	–0.031	0.084
30 (39)	0.043	0.226	0.017	–0.011	0.342*	0.116
40 (36)	0.117	0.221	0.025	–0.059	0.059	0.052
50 (33)	0.293	0.051	–0.264	–0.060	0.067	–0.027
Stem density, <5 cm dbh						
10 (45)	0.111	0.052	0.429*	–0.138	0.261	0.525*
20 (42)	–0.216	–0.070	0.331*	–0.150	–0.271	0.264
30 (39)	–0.085	–0.056	0.069	0.180	–0.415	0.422
40 (36)	–0.123	–0.049	0.120	–0.124	–0.087	0.308
50 (33)	–0.138	0.022	–0.039	0.303	0.281	0.075

Notes: The number of pairs is given in parentheses next to the lag distance. Significant autocorrelations at each lag distance are indicated by an asterisk.

* $P < 0.05$.

spatially autocorrelated data violate the assumption of independence of the sampling units. We tested for spatial autocorrelation in two size classes of woody vegetation (stem density <5 cm dbh, and stem density ≥10 to <25 cm dbh) using Moran's *I* statistic (GS+; Gamma Design Software, Plainville, Michigan, USA). These analyses showed weak or no significant autocorrelation of densities at lag distances from 10 to 50 m (Table 2). We also examined spatial autocorrelations in stem density and basal area in the other size classes, finding no significant patterns (data not shown). Given the lack of significant spatial structure in density and basal area at the quadrat level, we continued with traditional statistical methods to analyze the relationship between vegetation data and light data.

To compare tree allometry between forest types and among size classes, we performed two-way analysis of covariance (ANCOVA), using dbh or tree height as a covariate (main effects: forest type and diameter class). All variables were log transformed. We compared tree and crown dimensions among dominant species in both forest types using one-way ANCOVA.

We used multiple regression to examine the relationship between measures of forest structure and light availability at the 10 × 10 m quadrat level in both transects and plots. For transects, where we took light measurements at a single height level (0.75 m), optical density was regressed on basal area of stems ≥25 cm dbh and density of woody stems in four diameter classes (≥1 m tall to <5 cm dbh, ≥5 to <10 cm dbh, ≥10 to <25 cm dbh, and ≥25 cm dbh). Data for the three second-growth stands were combined, as were data for the three old-growth sites. We did not include the basal area of the smaller diameter classes since they were highly correlated with stem densities ($r^2 > 0.80$) and would cause multicollinearity in the models (Tabachnick and Fidell 1989).

In the plots we calculated mean tree height, maximum tree height, mean crown diameter, mean crown

area, and total crown area (sum of crown areas of all trees in the plot) for trees ≥10 cm dbh for each 10 × 10 m quadrat. Basal area and density of stems was calculated in three diameter classes (≥5 to <10 cm dbh, ≥10 to <25 cm dbh, and ≥25 cm dbh). Both plots within each stand were combined to increase sample size. We examined correlations among independent variables and eliminated those with correlation coefficients >0.70 to avoid problems with multicollinearity (Tabachnick and Fidell 1989). We regressed optical density on mean tree height, mean crown area, density of all stems ≥1 m tall and <5 cm dbh, and woody stem density in three diameter classes (≥5 to <10 cm dbh, ≥10 to <25 cm dbh, and ≥25 cm dbh).

RESULTS

Tree basal area and stem density

For transects, mean total basal area and density for all stems ≥5 cm dbh (diameter at breast height) was similar in second-growth and old-growth stands, with few significant differences in the means of ground-based vegetation data (Table 3). The basal area of stems in the intermediate tree size class (10–25 cm dbh) was significantly higher in second-growth forest ($P < 0.05$; Table 3). Stem densities <5 cm dbh were higher in the plot data set compared to transects because the plot samples also included herbaceous stems >1 m tall.

Canopy structure and tree architecture

When dbh was used as a covariate, second-growth trees were significantly taller (ANCOVA, $F_{1,595} = 6.98$, $P = 0.008$), whereas crown diameter did not differ significantly between forest types ($F_{1,597} = 1.86$, $P = 0.173$). When tree height was used as a covariate, second-growth trees had significantly smaller crown diameters than old-growth trees ($F_{1,595} = 5.51$, $P = 0.019$). Thus, as a group, second-growth trees had narrower crowns for their height and were taller for their diameter, compared to old-growth trees.

TABLE 3. Basal area (BA) and density of stems (no./ha) in four diameter classes and diffuse light transmittance along transects and in plots. .

Variable	Transect			Plot		
	Old-growth (<i>n</i> = 3)	Second-growth (<i>n</i> = 3)	<i>P</i>	Old-growth (<i>n</i> = 2)	Second-growth (<i>n</i> = 2)	<i>P</i>
Stem ≥ 5 to < 10 cm dbh						
BA (m ² /ha)	1.69 (0.10)	1.74 (0.22)	0.83	2.23 (0.03)	2.13 (0.12)	0.44
Stem density (no./ha)	411 (45.7)	456 (54.9)	0.28	530 (37.5)	517 (33.5)	0.44
Stem ≥ 10 to < 25 cm dbh						
BA (m ² /ha)	7.49 (0.33)	9.04 (0.69)	0.05	6.09 (1.88)	8.46 (0.91)	0.44
Stem density (no./ha)	408 (8.13)	488 (52.4)	0.28	313 (79.5)	471 (62.5)	0.73
Stem ≥ 25 cm dbh						
BA (m ² /ha)	21.39 (1.24)	19.01 (2.49)	0.51	26.82 (8.5)	11.59 (6.0)	0.12
Stem density (no./ha)	107 (3.81)	170 (47.3)	0.13	104 (21)	121 (8.5)	0.68
≥ 1 m tall and < 5 cm dbh						
Stem density (no./ha)	6095 (825.6)	6902 (772.73)	0.38	9258 (475)	8863 (1395)	1.00
Diffuse trans- mittance (%)	1.80 (109.44)	1.75 (47.54)	0.88	3.03 (0.05)	3.07 (0.01)	0.68

Notes: Data are means, with 1 SE in parentheses. Along transects, light was measured at 0.75 m in three old-growth and three second-growth stands. Plot data are from two plots in a second-growth stand (Lindero Occidental) and two plots in an old-growth stand (La Selva). In plots, light was measured at 1 m. *P* values are for Mann-Whitney *U* test for differences between forest types.

We also found strong effects of diameter class on crown dimensions. The two-way ANCOVA of crown diameter, using dbh as a covariate, revealed a highly significant interaction between forest type and diameter class ($F_{2,593} = 10.24$, $P = 0.00004$). Trees 10–25 cm dbh had significantly smaller crown diameters in second-growth forests (Tukey hsd; $P = 0.002$, Fig. 1B). Tree height varied significantly with diameter class in both forest types, but showed no significant interaction between forest type and diameter class (Fig. 1). Trees 10–25 cm dbh were significantly taller for a given tree diameter in second-growth than in old-growth stands (Tukey hsd; $P = 0.009$, Fig. 1B). Height at first branching also varied significantly with both forest type ($F_{1,591} = 9.29$, $P = 0.002$) and diameter class ($F_{2,591} = 9.11$, $P = 0.0001$) and showed a highly significant interaction with diameter class ($F_{2,591} = 4.80$, $P = 0.008$). This interaction also resulted from differences in trees 10–25 cm dbh, which branched higher in second-growth forest (Tukey hsd; $P = 0.00002$, Fig. 1B).

Second-growth trees differed allometrically from old-growth trees. The most pronounced differences were observed in trees in the 10–25 cm dbh class, whose crowns are located in the subcanopy or canopy. Forest-wide differences in tree allometry appear to be due to strong differences in species composition. Indeed, in the 10–25 cm dbh size class, tree species composition varied dramatically between the two forest types. *Casearia arborea* (Flacourtiaceae) and *Laetia procera* (Flacourtiaceae) were the most abundant species in the second-growth, composing 33% of all individuals in this diameter class. These dominant spe-

cies had small mean crown diameters (*C. arborea* = 5.5 m, *L. procera* = 4.1 m) that were significantly smaller for a given height compared to *Welfia regia* (Arecaceae) and *Pentaclethra maculosa* (Fabaceae), abundant old-growth dominants (ANCOVA, $F_{4,83} = 9.81$, $P < 0.0001$; Tukey's hsd, $P < 0.01$). In the old-growth stands, the subcanopy palm *W. regia* was the single most abundant species, with a mean crown diameter of 7.7 m. In addition, *L. procera* was significantly taller than *W. regia* for a given dbh (ANCOVA, $F_{4,160} = 16.05$, overall $P < 0.001$; Tukey's hsd, $P < 0.001$) and branched at greater heights compared to *P. maculosa* individuals in the 10–25 cm diameter class in old-growth stands (ANCOVA, $F_{4,83} = 9.81$, $P < 0.0001$; Tukey's hsd, $P < 0.01$). The allometric relationship between dbh and height was similar for *P. maculosa*, *C. arborea*, *L. procera*, and *Goethalsia meiantha* (Fig. 2A), whereas *W. regia* showed no significant relationship between dbh and height (data not shown). Species segregated by tree size along the same allometric line. *G. meiantha* trees were represented by large individuals, while *L. procera* and *C. arborea* were intermediate in size. *P. maculosa* trees spanned the entire size range (Fig. 2B). Thus, species differences in absolute tree size influenced overall crown dimensions and determined the species composition of different tree size classes.

Foliage profiles showed distinct patterns of vertical organization of vegetation between second-growth and old-growth stands. Second-growth forest had more foliage cover at 0–1 m and a lack of foliage above 30 m (Fig. 3A). Whereas foliage uniformly filled much of

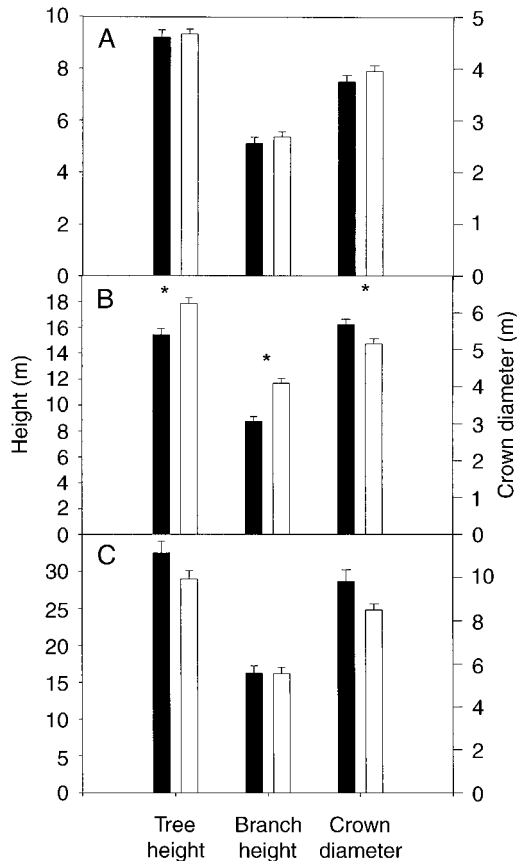


FIG. 1. Effects of stem diameter class on three growth variables for trees in second-growth (open bars) and old-growth (solid bars) sites in northeastern Costa Rica. Data are means and 1 SE. (A) Trees 5–10 cm dbh; (B) trees 10–25 cm dbh, and (C) trees ≥ 25 cm dbh. Asterisks indicate significant differences at the 0.05 level based on ANCOVA using dbh (tree and branch height) and tree height (crown diameter) as covariates.

the space above 2 m in old-growth forest (Fig. 3B; Old > Second; t test, $F_{1,3} = 8.47$, $P < 0.05$ after Bonferroni correction), the second-growth profile showed a gradual increase in foliage cover between 1 and 15 m. This pattern of distribution of foliage differed significantly between forests ($\chi^2 = 32.48$, $P < 0.0001$).

Vertical patterns of light availability

Along transects, mean light availability at 0.75 m height did not differ significantly between forest types (Table 3; see also Nicotra et al. 1999). Old-growth stands had a mean of 1.8% diffuse transmittance (% T) and ranged from 0.45–14.93% T ; second-growth stands ranged between 0.53 and 5.87% T with a mean of 1.75% T . Within plots, vertical profiles of diffuse transmittance increased from a mean of 2% at 1 m to >10% at 9 m (Fig. 4A). Ranges were similar at 9-m heights, with old-growth stands varying between 1.98 and 34.66% T , and second-growth stands between 1.57 and 33.57% T . At 1-m height the old-growth stands had a

higher minimum and maximum, ranging between 0.42 and 12.99% T ; whereas second-growth were 0.29–4.45% T .

Although means did not differ significantly between old-growth and second-growth stands (two-way ANOVA, interaction of main effects (height, forest type), $F_{4,255} = 0.276$, $P = 0.89$), the spatial autocorrelation function among heights differed markedly (Fig. 4B). In both forest types we observed a significant positive autocorrelation between points separated by one vertical meter (Moran's I : old-growth = 0.77, second-growth = 0.64, $P < 0.05$). Significant, positive autocorrelations persisted through a lag distance of four vertical meters in the old-growth plots. In contrast, the second-growth plots showed a transition to a significantly negative autocorrelation as vertical distance between points increased to 9 m (Moran's $I = -0.73$, $P < 0.05$). These results suggest that for sample points in the second-growth plots, higher values of light trans-

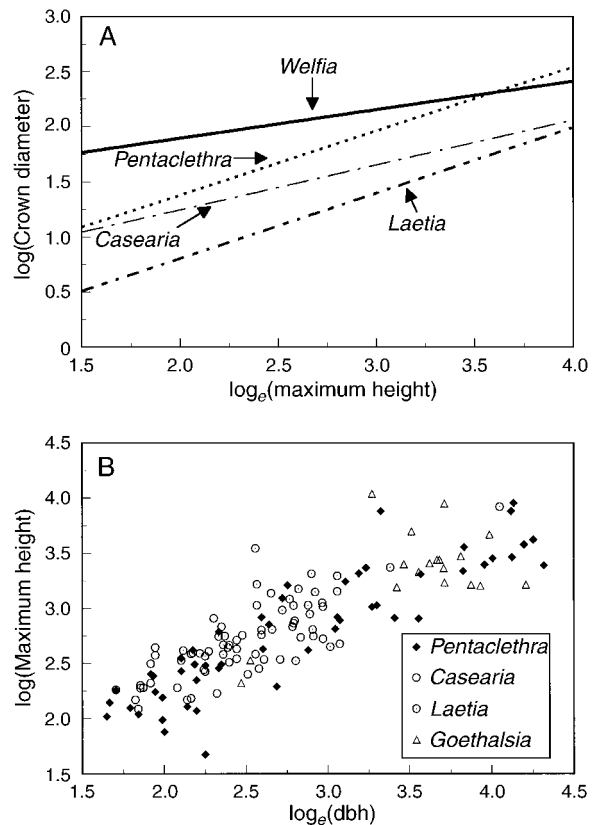


FIG. 2. Allometric relationships among five common species in three stands of old-growth forest and three stands of 15–20 yr old second-growth forest in the Caribbean lowlands of northeastern Costa Rica. (A) Regression lines of tree height (in meters) and crown diameter (in meters) for *Welfia regia*, *Pentaclethra macroloba*, *Casearia arborea*, and *Laetia procera*. (B) Scatterplot of tree diameter (in centimeters) and tree height (in meters) for individuals of *Goethalsia meiantha*, *P. macroloba*, *C. arborea*, and *L. procera*. Each point represents a single tree.

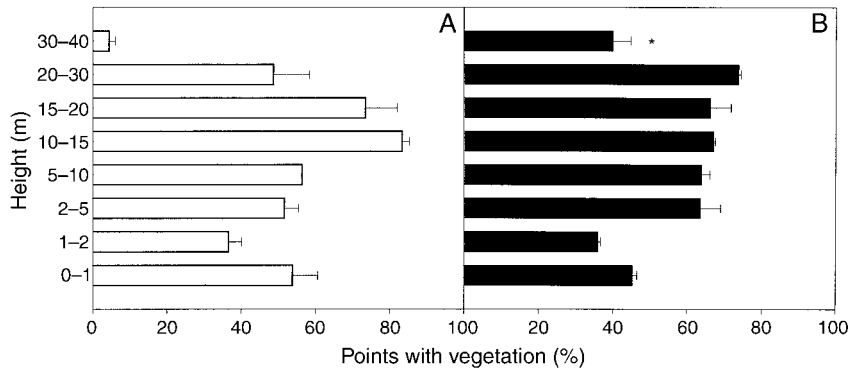


FIG. 3. Foliage height profiles in (A) three stands of 15–20 yr old second-growth forest and (B) three stands of old-growth forest in the Caribbean lowlands of northeastern Costa Rica. The asterisk indicates a significant difference between old- and second-growth forests (*t* test; $P < 0.05$ after Bonferroni correction). Data are means and 1 SE.

mittance at heights of 9 m were associated with lower light transmittance at heights of 1 m.

Light availability and forest structure

Within a given forest type (old or second-growth), light availability at points 0.75 m above the forest floor

was most strongly influenced by the density of saplings and shrubs (woody stems ≥ 1 m tall and < 5 cm dbh) (Table 4). As the density of saplings and shrubs increased, optical density increased (light availability decreased). Although individual predictor variables were significant, the explanatory power of the overall models was extremely low, with R^2 values of 0.17 and 0.03 for old-growth and second-growth stands, respectively.

Multiple regressions using plot data for optical density at multiple heights proved more informative. Vegetation-structure variables explained 7–42% of the variance in optical density for old-growth stands, compared to $< 2\%$ in second-growth stands. In general, regression models in the old-growth forest site were similar at all heights and included positive relationships between the stem density 5 to 10 and 10–25 cm dbh and optical density (Table 5). Stem density 10–25 cm dbh was a significant predictor of light availability at 1 m ($P = 0.024$), 6 m ($P = 0.05$) and 9 m ($P = 0.001$), while stem density 5–10 cm dbh was a significant predictor at 2 m ($P = 0.02$) (Table 5). The second-growth site showed little correspondence between vegetation-structure variables and optical density at heights < 9 m. Multiple-regression models for second-growth stands were not significant at any height (Table 5).

General patterns in the multivariate data set can be visualized using the bivariate relationships between stem density 10–25 cm dbh and optical density at each height (Fig. 5). In the old-growth stand, increased density of stems 10–25 cm dbh was associated with increased optical density (decreased light availability) at all heights. In contrast, the second-growth stand showed no relationship between tree density and optical density at heights < 6.5 m (Fig. 5). At 6.5 m and 9 m heights, optical density increased as density increased, as in the old-growth stand, although this relationship was considerably weaker in the second-growth stand.

DISCUSSION

Our data demonstrate subtle, but ecologically significant, differences in the physical structure of second-

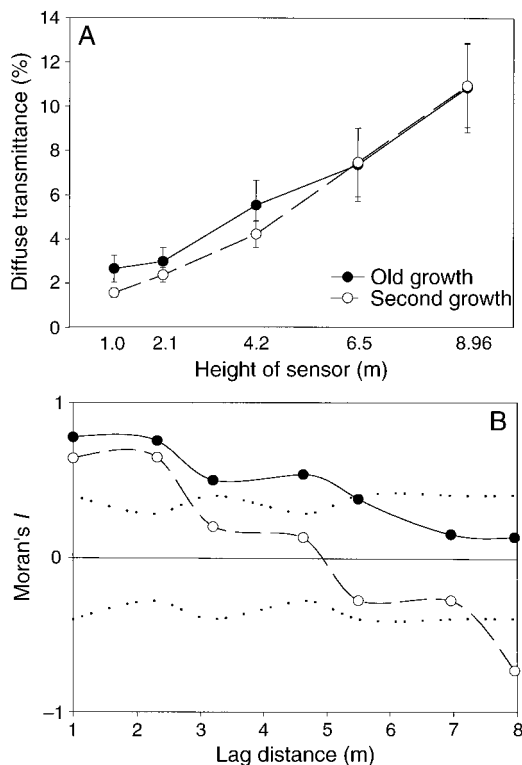


FIG. 4. Patterns of vertical light availability in an old-growth forest and a 15–20 yr old second-growth forest at La Selva Biological Station, in the Caribbean lowlands of northeastern Costa Rica. (A) Diffuse transmittance at five heights above the forest floor; data are means ± 1 SE. (B) Moran's *I* at five vertical lag distances (see *Methods: Light availability and Statistical analysis*). Dotted lines represent 95% confidence intervals.

TABLE 4. Results from multiple-regression models of the relationship between measures of forest structure (stem density in four size classes: ≥ 1 m tall and < 5 cm dbh, 5–10 cm dbh, 10–25 cm dbh, and ≥ 25 cm dbh; basal area ≥ 25 cm dbh) and diffuse light transmittance for old-growth and 15–20 yr old second-growth stands in the Caribbean lowlands of northeastern Costa Rica.

Model	df	R^2	P	Predictor	Partial correlation
Old-growth	5, 123	0.170	0.0001	stem density (≥ 1 m tall and < 5 cm dbh)	0.414
Second-growth	5, 138	0.027	0.117	stem density (≥ 1 m tall and < 5 cm dbh)	0.198

Notes: The dependent variable in all models was optical density, the inverse log of percentage transmittance. Optical density increases with decreasing light availability; thus a positive coefficient indicates a negative relationship. Significant predictors ($P < 0.05$) are shown even when the overall model was not significant.

and old-growth forests that influence spatial variation in light transmittance in the understory. These relationships are challenging to detect, given the complexity of tropical-forest species composition and structure. Mid-sized trees (10–25 cm dbh) have higher basal area in the second-growth forests. These mid-sized stems differ in species composition between forest types and these species, as a group, possess contrasting allometry and crown sizes. These characteristics contribute to observed differences in the vertical organization of vegetation and in the pattern of horizontal variation in light transmittance (Nicotra et al. 1999). Collectively, the differences in forest physical structure influence the strength of the relationship between canopy vegetation and transmittance of light in the understory. The more homogeneous size distribution and species composition of the second-growth forest canopy and subcanopy layers are associated with increased spatial homogeneity of diffuse light transmittance within the understory, compared to old-growth stands.

Physical structure: old-growth vs. second-growth

Basal area can recover rapidly in second-growth forests after only 15–20 yr of regrowth, while canopy height and canopy species diversity lag behind (Fig. 3; Guariguata et al. 1997, Guariguata and Ostertag, *in press*). Foliage profiles show that second-growth stands are still in a “building” phase of structural development. Old-growth stands are of higher stature, have less vegetation near the forest floor, and show a more even distribution of foliage vertically (Fig. 3). Our data corroborate other chronosequence studies in both temperate and tropical wet forests that have shown an increasing vertical spread of vegetation in the profile as stands develop (Terborgh and Petren 1991, Brown and Parker 1994, Denslow and Guzman 2000).

Tree architecture and light transmission

Crown architecture and tree allometry reflect diverse species-specific solutions to the allocation of limited biomass between support structures and the photosyn-

TABLE 5. Results of multiple-regression models of the relationship between measures of forest structure and diffuse light transmittance at six heights above the forest floor for one old-growth (La Selva) and one 15–20 yr old second-growth stand (Lindero Occidental) in the Caribbean lowlands of northeastern Costa Rica.

Model height (m)	df	R^2	P	Predictor	Partial correlation
Old-growth					
1	6, 16	0.252	0.090	stem density (10–25 cm dbh)	0.529
2.1	6, 16	0.246	0.100	stem density (5–10 cm dbh)	0.544
4.2	6, 16	0.071	0.316	no significant predictors	
6.5	6, 16	0.084	0.298	stem density (10–25 cm dbh)	0.461
9	6, 16	0.415	0.019	stem density (10–25 cm dbh)	0.738
Second-growth					
1	2, 21	0.001	0.472	no significant predictors	
2.1	2, 21	0.001	0.733	no significant predictors	
4.2	2, 21	0.001	0.608	no significant predictors	
6.5	2, 21	0.001	0.719	no significant predictors	
9	2, 21	0.04	0.367	no significant predictors	

Notes: Dependent variable in all models was optical density, the inverse log of percentage transmittance. Optical density increases with decreasing light availability, thus a positive coefficient indicates a negative relationship. Significant predictors ($P < 0.05$) are shown even when the overall model was not significant.

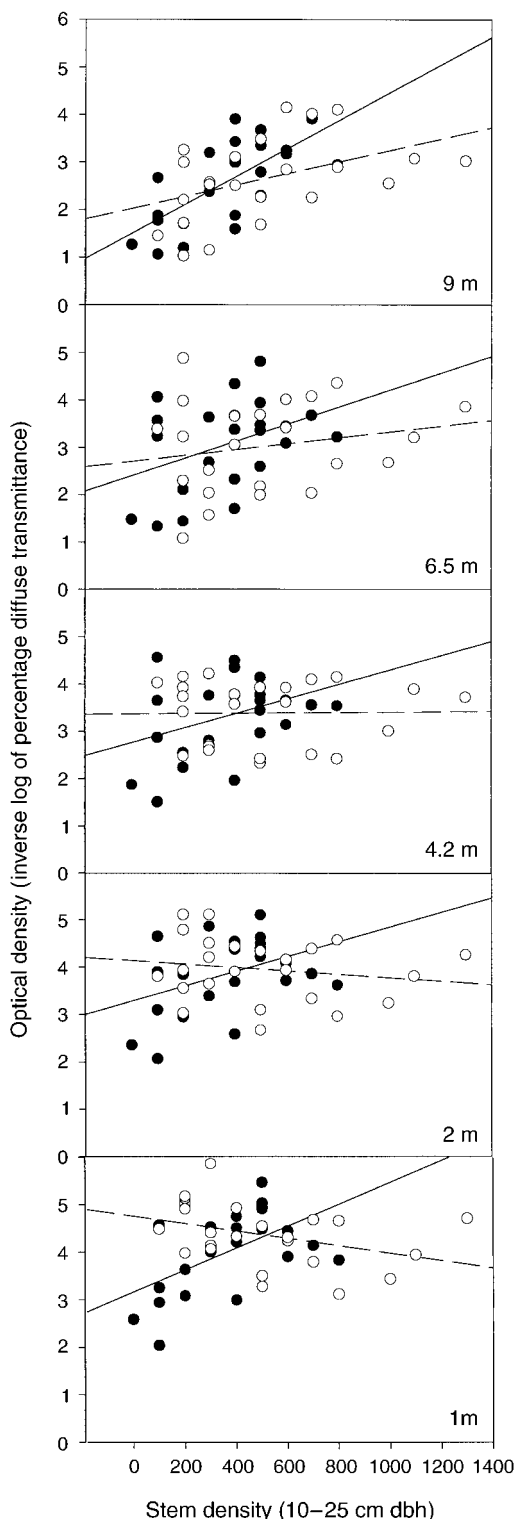


FIG. 5. Bivariate relationships between diffuse light transmittance at five heights above the forest floor and the density of stems 10–25 cm dbh in an old-growth (●, solid lines) and a second-growth (○, dashed lines) stand at La Selva Biological Station, in the Caribbean lowlands of northeastern Costa Rica.

thetic apparatus (Horn 1971, Givnish 1982, King 1987, 1996, Sterck and Bongers 1998). Fast-growing, early successional tree species tend to grow rapidly in height, forming slender stems and compromising safety for a rapid arrival to the canopy. Alternatively, shade-tolerant trees regenerating beneath an existing canopy tend to form wider crowns, efficiently capturing light and increasing in stem diameter as they gradually approach the canopy (King 1990). Finally, relationships among tree height, stem diameter, and crown diameter, shift as trees increase in overall size and canopy position (King 1996, Sterk and Bongers 1998).

Differences in species composition and tree size strongly influence the physical structure of the stands in our study. Differences in tree dimensions are most pronounced in the 10–25 cm dbh class. Thus, in addition to being more abundant, mid-size stems also diverge most in crown architecture between forest types (Figs. 2 and 3). Forest-wide differences in crown architecture arise, in part, from dominance by particular species. While systematic differences in tree size and allometry do play a critical role in the differentiation of the physical structure of old-growth and second-growth forests, can these differences also affect light transmission?

The high species richness of trees and the complex vertical structure of tropical rain forests create difficulties in assessing the impact of species-specific allometry on patterns of light transmittance. In a study conducted at La Selva Biological Station in second-growth stands dominated by single species, Kabakoff and Chazdon (1996) found species-specific effects on understory light availability. That study was conducted in areas of similar history, age, and species composition to the second-growth stands described here. Dominant canopy species *Goethalsia meiantha* and *Pentaclethra macroloba* diverged strongly in tree allometry, with *G. meiantha* having taller stems for a given diameter and small crowns for a given height (Kabakoff and Chazdon 1996, King 1996). In that case, canopy trees indirectly influenced understory light through differential effects on growth of sub-canopy and understory vegetation. *G. meiantha*'s narrow, globular crown allowed greater light penetration below the canopy, increasing the density of understory shrubs and saplings, and ultimately leading to lower light availability at 1 m height.

Light transmittance and heterogeneity in relation to forest structure

We observed little or no direct effects of the canopy vegetation on variation of optical density near the forest floor within old-growth or second-growth forests (Table 4). In both forest types the only significant predictor of optical density at 0.75 m was the density of woody shrubs and saplings (stems >1 m tall and <5 cm dbh, Table 4). Across a tropical moist chronosequence, Denslow and Guzman (2000) found no relationship between mean stand light levels or coefficient of variation

of light levels within stands, despite changes in forest structure. Similarly, Brown and Parker (1994) found that stem-based measurements of trees offered little predictive power when examining changes in light availability near the forest floor across a chronosequence in temperate deciduous forest. They suggested that crown-based measurements, such as foliage density and leaf-area index, may be more informative in a tropical moist forest sequence. Alternatively, canopy vegetation structure may indirectly influence understory light availability, through impacts on subcanopy and understory vegetation (Kabakoff and Chazdon 1996).

The lack of a strong relationship between canopy or subcanopy vegetation and light transmittance in the understory reflects distinct spatial patterning in these variables. Although diffuse light transmittance in these forests is strongly spatially autocorrelated at scales below 20 m (Nicotra et al. 1999), we found little or no spatial autocorrelation in vegetation density in any forest stand (Table 2). In old-growth stands at La Selva, Clark et al. (1996) found that canopy height was significantly autocorrelated at 2.5-m intervals (smaller than our sample unit), but even at that scale, correlations between canopy height and understory light availability were weak. Thus, light transmittance varies on a fine spatial scale among understory microsites, whereas vegetation structure of canopy and midstory trees shows little or no spatial patterning at scales below 50 m (Table 2). Vegetation composition and structure does show pronounced spatial variation at larger spatial scales due to edaphic factors (Clark et al. 1995, 1998, 1999). These landscape-level vegetation patterns may influence patterns of light transmittance in the understory at scales larger than that examined in our study (Clark et al. 1996, Kabakoff and Chazdon 1996). Thus, while forest structure may be an important predictor of light availability at large spatial scales (across forest stands that differ in basal area and species composition), we conclude that it is not a useful predictor of light availability within stands or across stands that are similar in gross physical structure. At these finer scales, more subtle factors such as tree architecture, species composition, and vertical distribution of foliage may be more influential.

Vertical patterns of light and forest structure

Assessment of vertical patterns of light availability in plots permitted a more detailed analysis of the relationship between light transmittance and forest structure (Fig. 4). In vertical as well as horizontal directions we found that mean light availability inadequately characterizes the complexity of second-growth and old-growth stands, which differed in both variance and spatial pattern of light (Fig. 4; Nicotra et al. 1999). Mean levels of light availability at all heights above the forest floor mask differences in the spatial relationships among heights in old-growth and second-growth stands. Vertical patterns of light transmission provide

evidence for the existence of recent, complete-canopy-to-forest-floor gaps in old-growth stands and their absence in second-growth stands.

The absence of large treefall gaps in second-growth stands reflects a number of forest dynamic processes, as noted by Brokaw (1982b), Yavitt et al. (1995), and Connell et al. (1997). Treefalls by small-crowned second-growth trees may not have the volume or size to create complete gaps from canopy to forest floor. Indeed, creating large artificial canopy gaps of 350–450 m² in 15–20 yr old second-growth at La Selva, requires cutting at least 15 canopy trees (J. M. Dupuy and R. L. Chazdon, *personal communication*). Mortality of many early successional trees occurs after they become overtopped. When these overtopped individuals die, no canopy gaps are created. Rather, they leave behind an empty space, or a “sub-canopy gap” below the upper canopy layer (Connell et al. 1997). These second-growth forests can therefore be viewed as having an essentially two-tiered structure—the young, building-phase forest growing beneath a closed canopy of long-lived, fast-growing trees that established early in secondary succession (Guariguata and Ostertag, *in press*).

What are the causal mechanisms for differences in vertical distribution of light and its changing relationship to vegetation? We hypothesize that second-growth forests (15–25 yr old) and old-growth forests differ in stand dynamics, leading to distinct patterns of vertical organization of vegetation and vertical distribution of light. At the stand level, light conditions in the understory of old-growth forests reflect the constant gap-formation and gap-filling process of old-growth forest dynamics. In mature tropical rain forests, tree falls or branch falls by canopy or emergent trees with large, spreading crowns cause complete gaps that extend from the forest floor to the canopy (Brokaw 1982a, Connell et al. 1997). Spatial-autocorrelation analysis confirms that these gaps influence light over horizontal distances twice as large as that in second-growth forests (Clark et al. 1996, Nicotra et al. 1999).

In contrast, slender trees with small crowns dominate second-growth stands. Light penetrates through numerous, small, evenly distributed openings throughout the canopy hemisphere, with little open sky concentrated near the zenith (Nicotra et al. 1999). This pattern of canopy structure is associated with enhanced overall diffuse light availability and increased spatial homogeneity compared to old-growth stands (Nicotra et al. 1999). Vertical profiles of foliage and light availability suggest that tree recruitment in second-growth stands involves vertical filling of openings created below the canopy.

Our hypotheses regarding forest development in second-growth tropical rain forests require a rigorous examination of the relationship between light transmittance and the three-dimensional distribution of foliage (Parker and Brown 2000). The questions initially raised in this paper were left only partially answered by our

static measurements of forest structure and light transmittance. Long-term studies in larger plots, comparing the vertical structure of mature and second-growth forests, would provide data to explore our hypothesis that vegetation dynamics in young stands involve recruitment in sub-canopy gaps below the canopy. These studies are currently underway in northeastern Costa Rica. The results presented here challenge the view that forest-dynamic processes are driven by direct effects of canopy trees on understory light environments, especially in young, second-growth forests. This expanded view of tropical rain forest dynamics is critical for understanding forest regeneration in the land-use mosaic of today's tropics.

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