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Crown light environments of saplings of two species of rain forest emergent trees

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Summary. The crown light environments of saplings of two Costa Rican rain forest tree species were simultaneously compared. The species, *Dipteryx panamensis* (Pitt.) Record & Mell., a relatively shade-intolerant species, and *Lecythis ampla* Miers, a shade-tolerant species, have contrasting growth and branching patterns. Quantum sensors were placed throughout the crowns of saplings up to 2.5 m tall and quantum fluxes were recorded with microloggers for seven-day periods. The shade-intolerant species had total quantum flux densities 35% larger than those of the shade-tolerant species, but totals for both species were less than 2% of full sun. More than 90% of the quantum flux densities measured within the crowns of both species were less than 25 μmol m^{-2} s^{-1}. Lateral light was an important component of daily quantum flux totals; for saplings of both species, the half-hour with the maximum average irradiance for the day frequently occurred in mid-morning or mid-afternoon. Despite dissimilar crown and leaf display, there was no difference in the overall variability of irradiance within the crowns of the two species. However, quantum fluxes received within the crowns differed substantially in both species. Within-crown locations differed significantly from day to day because of variation in weather conditions. Daily total quantum flux densities and totals expressed as a percent of full sun were significantly correlated with height growth over the previous 12 months.

Key words: *Lecythis* – *Dipteryx* – PPFD – Rain forest

The importance of treefall gaps in tropical forest regeneration has been the subject of considerable investigation, particularly with reference to the hypothesized role for gaps in the maintenance of tropical tree diversity (Whitmore 1975, 1978; Hartshorn 1978, 1980; Denslow 1980; Bazzaz 1984; Brokaw 1985). Tropical tree species are thought to differentially utilize the assortment of microenvironments introduced into the understory by treefalls of various sizes (Denslow 1980). Functional classifications of tree species have been based on the perceived gap requirements for regeneration (Hartshorn 1978; Bazzaz 1984), particularly with respect to irradiance, the resource most strongly affected by treefalls. However, the increase in irradiance resulting from a treefall gap can be relatively short-lived compared to the probable length of time required for saplings to escape the low irradiances in the understory (Clark and Clark 1987a). In spite of the great theoretical interest in this topic, there are few data available that assess light environments within rain forest (Evans et al. 1960; Yoda 1974, Chazdon and Fetcher 1984), and more importantly, the environments occupied by individual species (Björkman and Ludlow 1972; Pearcy 1983; Chazdon 1986). The goal of this research was to quantify the magnitude and variation of photosynthetically active radiation reaching the leaves of saplings of two dissimilar species of rain forest trees. Furthermore, we wanted to determine if short-term measurements of crown light environments could be related to long-term growth.

The species examined in this study, *Dipteryx panamensis* (Pitt.) Record & Mell. and *Lecythis ampla* Miers, are both emergents in the Atlantic lowlands of Costa Rica attaining diameters greater than 1.5 m and heights up to 45 m. Saplings differ considerably in terms of crown architecture, leaf size, and leaf display patterns. Crowns of sapling *Dipteryx* are relatively flat with a single orthotropic stem and large plagiotropic compound leaves consisting of leaflets 40–100 cm^2 in area. In contrast, crowns of sapling *Lecythis* are composed of a complex array of branches and small leaves (10–15 cm^2).

Saplings of both *Dipteryx* and *Lecythis* are uncommon in primary forest. Different regeneration patterns have been hypothesized for these species (Hartshorn 1978; Clark and Clark 1987a). Hartshorn (1978) categorized *Dipteryx* as a gap-dependent species. Clark and Clark (1987b) reported that while *Dipteryx* can germinate and establish in the understory in the absence of a gap, only those juveniles under fairly open sites show substantial growth. *Lecythis* is considered a shade-tolerant species (Clark and Clark 1987a). Both species are part of a long-term study of the demography and ecophysiology of rain forest trees (Clark and Clark 1987a).

Materials and methods

Study site

The study was conducted at the La Selva Biological Station of the Organization for Tropical Studies in the Atlantic lowlands of Costa Rica (83° 59′W, 10° 26′N). The vegetation at La Selva is classified as tropical wet forest (Hartshorn 1983). The forest at La Selva is very dynamic with

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large branch and treefalls a common occurrence. The turnover time has been estimated to be slightly more than 100 years (Hartshorn 1978). A detailed description of the site can be found in Hartshorn (1983). Rainfall totals about 4 m annually and averages more than 100 mm per month. The period from January to April is distinctly drier than the remainder of the year (La Selva, unpublished records). Measurements in the present study were made from 12 April to 15 July 1986, which corresponds to the late dry season-early wet season.

Light environment within sapling canopies

Photosynthetic photon flux densities (PPFD) were measured with microloggers (Campbell 21 X, Campbell Scientific Inc., Logan, Utah) using gallium arsenide phosphide (GaAsP) photodiodes (PH201A, NEC Electronics, Mountainview, California) as sensors (Gutschick et al. 1985; Chazdon and Field 1987). Millivolt outputs of the photodiodes were measured across a 510 ohm resistor. Sensors were calibrated against a quantum sensor (Li-190, Li-Cor Inc, Lincoln, Nebraska) under both sky and a metal-halide multivapor lamp. The relationship between PPFD as determined by the Li-Cor sensor and the output of the photodiodes were linear ($r^2 \geq 0.99$) and similar under both sky and artificial light. Lamp calibration values were used for the data presented here. Sensors were recalibrated every 14 days of use.

Sensors were scanned at 5 s intervals and the data were recorded on magnetic cassette tape as means, maxima, minima, and histograms at 30 min intervals between 0430 and 1830 h solar time. Histograms stored the frequency distribution of PPFD in 25 μmol m^{-2} s^{-1} bins between 0 and 1000 μmol m^{-2} s^{-1}. Photosynthetic photon flux densities were simultaneously recorded for all but four days of the study period in a large clearing (henceforth referred to as full sun) using a micrologger (Campbell CR 21) and a quantum sensor (Woodward and Yaquib 1979).

Species were compared by simultaneously measuring the light environment of one sapling of each species over a seven-day period. Ten different pairs were measured over the course of the study. Saplings were selected from populations growing in undisturbed forest. All saplings were under at least one tree canopy and most were under more than two canopies. Locations of saplings ranged from building phase forest in old gap sites to closed canopy. Saplings were matched according to general size and growth performance; saplings with similar relative intraspecific rank in height growth from 1985 to 1986 were paired. The saplings measured were chosen to represent the maximum range of growth observed for these species in the primary forest.

Fifteen or sixteen photodiodes were mounted adjacent to leaves within the crowns of each sapling to be measured. Sensors were positioned to provide the most even distribution of sensors over the leaf area of a sapling and were oriented to the same angle and azimuth as that of the nearest leaf, or leaflet in the case of *Dipteryx*. Sensors were not mounted directly through the leaves as per Gutschick et al. (1985) because the plants were part of a long-term study of growth and leaf demography. Sensor positions were checked daily in the morning; sensors that had been dislodged or covered by falling debris were eliminated from the previous day's analysis. Angles and azimuths of all sensors and their positions within the sapling canopy were determined at the end of the seven-day measurement period. Mean sensor deviations from horizontal over the course of the study were $12.0 \pm 7.8°$ for *Lecythis* and $15.7 \pm 13.5°$ for *Dipteryx*. The distributions of sensor azimuths for the two species did not significantly differ each other or from a uniform distribution.

The base data set for each sensor consisted of the average and the frequency distribution of 360 PPFD samples taken every half-hour. A mean daily sensor total and standard deviation derived from the 28 half-hour totals were calculated by averaging the half-hour totals, and daily sapling totals were calculated by averaging the daily sensor totals. Daily sapling totals were also expressed as the percentage of full sun by dividing by the full-sun total PPFD for that day. Weekly sapling totals were calculated by averaging the 7 daily plant totals. Statistical analyses were made using STATISTIX, a MS-DOS software package (NH Analytical Software, St. Paul, Minnesota).

Leaf area and crown structure

Total sapling leaf area and its overall arrangement on the plant were estimated at the end of the seven-day measurement period. Leaf areas of *Dipteryx* were determined by measuring the area of leaf tracings. Because of the large numbers of leaves per sapling (up to 681), leaf areas for *Lecythis* were estimated by measuring the length and width of a subsample of 10% or more of the leaves, computing the average dimensions, and applying a regression of leaf area against leaf length and width ($r^2 = 0.95$) to obtain average area per leaf. The total sapling leaf area was then estimated by multiplying the total number of leaves on the sapling by the calculated area per leaf. Crown area, that is, the area that a vertical projection of the crown would cover, was estimated by measuring the furthest projections of leaves or branches from the stem in each direction and assuming the crown formed an irregular polygon. Crown volumes were estimated by multiplying the distance between the highest and lowest leaves by the crown area.

Results

Comparisons between species

Dipteryx and *Lecythis* saplings measured in this study did not differ significantly in terms of mean height, mean diameter, mean height growth 1985–1986, mean diameter growth 1985–1986, and estimated leaf area (Table 1). However, mean leaf area of *Lecythis* was nearly twice that of *Dipteryx*. Mean crown area and crown volume of *Lecythis* were more than twice those of *Dipteryx* (Table 1).

Total PPFD in full sun averaged 30 moles m^{-2} d^{-1} (CV 33.6, range 9.5–48.3 moles m^{-2} d^{-1}, $N = 66$ days) during the study period. Saplings of both species in the forest received less than 2% of the full sun total (Table 2). When all 70 days of the study period were treated as independent samples, the median total daily PPFD for *Dipteryx* was significantly higher than that for *Lecythis* ($P < 0.04$, $N = 70$, Kruskal-Wallis non-parametric ANOVA). However, when weekly totals were compared, the difference between species in terms of the PPFD received was not significant because of the lower effective sample size ($P > 0.23$, $N = 10$).

More than 90% of the measured PPFDs within the crowns of both species were less than 25 μmol m^{-2} s^{-1}

Table 1. Growth and morphological characteristics of *Dipteryx panamensis* and *Lecythis ampla* saplings measured for light environment

	Dipteryx			*Lecythis*		
	Mean	Min	Max	Mean	Min	Max
Height (cm)	134	89	209	142	98	235
Diameter (mm)	9.5	5.4	13.3	12.3	8.2	21.0
Height growth 1985–86 (cm)	19.0	−24.3	58.4	10.0	−24.1	45.5
Diameter growth 1985–86 (mm)	1.2	0.2	3.4	1.4	0.4	3.9
Number of leaves or leaflets	43*	20	81	285*	45	681
Leaf area (cm^2)	1900	329	5791	3680	348	11380
Crown area (cm^2)	3862	623	15630	7643	736	26380
Crown volume (m^3)	0.22	0.01	1.11	0.92	0.02	4.48

* Significantly different at $P<0.05$

Table 2. Daily irradiance totals for saplings of *Dipteryx panamensis* and *Lecythis ampla*. Medians are based on 7 days observation of ten individuals per species

	Total daily PPFD (moles m^{-2} d^{-1})				Daily % of full sun			
	Median	CV	Range	*N*	Median	CV	Range	*N*
Dipteryx	0.42*	127	0.11 to 4.11	70	1.5*	100	0.4 to 10.6	66
Lecythis	0.31*	69	0.14 to 1.60	70	1.1*	57	0.7 to 5.0	66

* Significantly different at $P<0.05$

(Fig. 1). The percentage was slightly higher for *Lecythis* (95.3%) than for *Dipteryx* (93.3%). If PPFD values greater than 50 μmol m^{-2} s^{-1} are considered sunflecks, then saplings of *Dipteryx* received an average of 19.1 min of sunfleck per day versus 18.1 min for *Lecythis*. The mean frequency distributions for *Dipteryx* and *Lecythis* were significantly different ($P<0.03$, Kolmogorov-Smirnov test) as were 7 of the 10 pairwise comparisons. The distributions differed most at PPFD less than 100 μmol m^{-2} s^{-1}. With the exception of the 0 to 25 μmol m^{-2} s^{-1} interval, variation in the frequency distributions of both species was substantial (Table 3). The coefficients of variation above 25 μmol m^{-2} s^{-1} ranged from 78 to 219, and were lower for *Dipteryx* than for *Lecythis* over most of the range.

Intra-crown variability

Variability in PPFD measured within the crowns of both species was large. For both *Lecythis* and *Dipteryx* saplings,

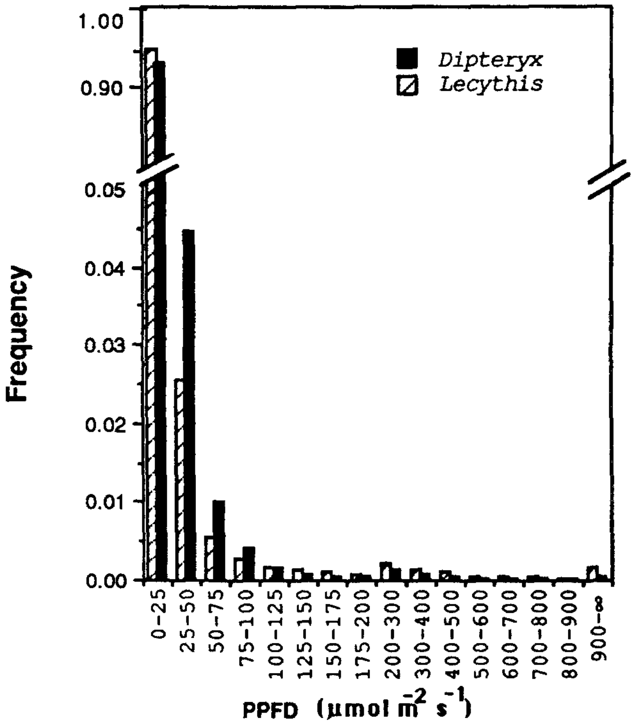

Fig. 1. The mean frequency distribution of photosynthetic photon flux densities within the crowns of saplings of *Dipteryx panamensis* and *Lecythis ampla*. $N=10$. Note change in scale of y-axis and increase in histogram interval above 200 μmol m^{-2} s^{-1}

Table 3. Coefficients of variation for frequency distributions of PPFD within the crowns of saplings of *Dipteryx panamensis* and *Lecythis ampla*. $N=10$

Range of PPFD μmol m^{-2} s^{-1}	*Lecythis* CV	*Dipteryx* CV
0–25	6.4	8.8
25–50	146.5	111.1
50–75	120.9	195.2
75–100	126.8	182.4
100–125	130.5	133.0
125–150	136.8	80.4
150–175	139.1	80.9
175–200	137.6	79.5
200–300	149.7	78.1
300–400	162.6	79.0
400–500	173.1	92.5
500–600	178.6	108.7
600–700	187.3	120.5
700–800	196.1	129.6
800–900	202.3	150.7
900–∞	219.2	131.7

the ratio of maximum to minimum sensor (site within the crown) in terms of total PPFD averaged about 5.5; the daily coefficient of variation of totals among sensors averaged 135. Intra-crown variability in terms of the coefficients of variation of sensor daily total PPFD, the coefficients of variation of sensor daily percentage of full sun, the daily ratio of maximum to minimum sensor, and the daily range between maximum and minimum sensors did not differ significantly between species (Table 4).

Table 4. Results of one-way nonparametric ANOVA of intra-crown variability in irradiance for saplings of *Dipteryx panamensis* and *Lecythis ampla*. $N = 66$ to 70 per species

	Dipteryx Mean	*Lecythis* Mean	F	*P*
Coefficient of variation of daily mean PPFD	128.7	140.9	0.29	0.60
Coefficient of variation of daily mean % full sun	130.4	141.8	0.14	0.68
Daily ratio of maximum to minimum sensor	4.0	6.9	0.87	0.36
Daily range between maximum and minimum sensor (μmol m^{-2} s^{-1})	12.6	14.5	0.24	0.63

To test the significance of the variation in irradiance at the level of the individual sapling, non-parametric two-way analysis of variance of the daily sensor totals was performed for all plants using time (7 days) and sensor (location within the crown) as the categorical variables. For all 20 saplings, there was highly significant variation ($P < 0.005$) among days and among sensors. Thus, significantly different light environments were always obtained at different locations within the crowns of these 0.9 to 2.5 m tall saplings.

The large variation in sapling light environment was related to weather conditions and time-dependent events. The daily total at each plant was positively correlated with the full sun total (Spearman's $r_s = 0.48$, $P < 0.005$), as was the coefficient of variation of daily total PPFD among sensors ($r_s = 0.58$, $P < 0.005$). Thus higher irradiance outside the forest generally led to greater irradiance received within the forest, as well as more variable light environments at each sapling.

The time of the maximum half-hour average PPFD usually occurred within 1.5 h of solar noon (Fig. 2). A significant fraction of half-hour maxima also occurred in mid-morning (0930 h) and mid-afternoon (1500 h), although values in the full sun were without such subsidiary peaks (Fig. 2). These morning and afternoon maxima indicate that low-angle, lateral light from canopy openings located to the side of the saplings, as well as light from openings directly above, made an important contribution to the daily total PPFD. Both morning and afternoon peaks consisted of contributions from ten of the twenty saplings. Two-way non-parametric analysis of variance was performed on each individual sapling's times of maximum irradiance over the seven-day period, using days and sensor (location) as the categorical variables. For all 20 saplings, the day effect was highly significant ($P < 0.01$), that is, the time of maximum irradiance varied significantly among days for all plants. For three of the *Dipteryx* and seven of the *Lecythis*, there was also a significant sensor effect, that is, the times at which individual locations within the crown received their maximum half-hour of irradiance differed (data not shown).

Correlations with growth and crown characteristics

Diameter and height growth increments from 1985 to 1986 and sapling leaf area were correlated with the daily totals

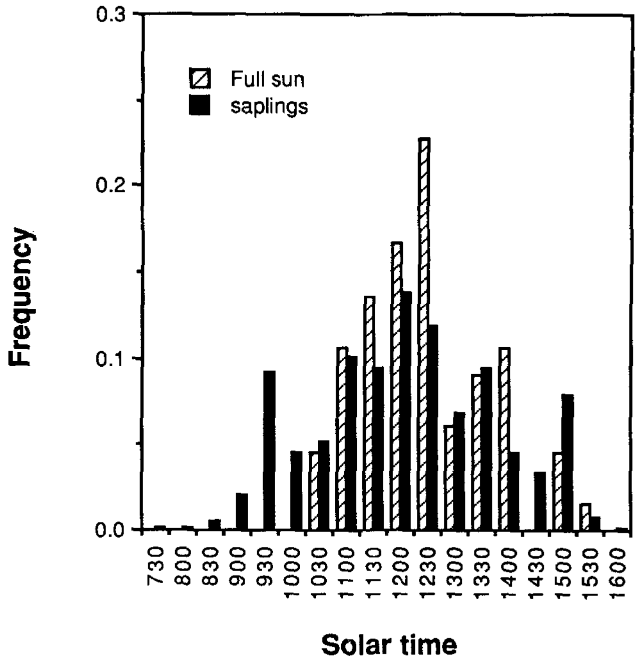

Fig. 2. The distribution of times of occurrence for the daily maximum half hour of mean PPFD in full sun ($N = 66$ days) and within the crowns of *Dipteryx panamensis* and *Lecythis ampla* (all sensors combined, $N = 2143$ sensor-days)

of PPFD and the weekly mean percentage of full sun (Table 5). Height growth of *Lecythis* was significantly correlated with both measures of light environment. Height growth and leaf area of *Dipteryx* were significantly correlated with percentage of full sun. For all combinations of species and growth index, correlations with mean percentage of full sun were higher than correlations with weekly total quantum flux density. Height growth of *Lecythis* but not *Dipteryx* was significantly correlated with the proportion of PPFD from sunflecks, that is, PPFD greater than 50 μmol m^{-2} s^{-1}. Sapling leaf area was significantly correlated with diameter and height growth with one exception, the diameter increment of *Lecythis* (Table 5). Correlations of height and diameter growth with weekly intercepted irradiance on a leaf area basis (mean weekly PPFD × sapling leaf area) were similar to those with leaf area alone (Table 5).

Crown area, crown volume, and sapling height were not significantly correlated with total PPFD for either species (Table 6). However, mean percentage of full sun was significantly correlated with crown volume of both species and with crown area and sapling height for *Lecythis*. Correlations between coefficients of variation of mean sensor total PPFD (intra-crown variability) and sapling height, crown area, and crown volume were significant for *Dipteryx* but not for *Lecythis*.

Discussion

The difference between the light environments of *Dipteryx* and *Lecythis* measured in the present study was smaller than expected considering that *Dipteryx* has been classified as gap-dependent species (Hartshorn 1978). Because saplings of both of these species show similar growth under light levels comparable to understory – not gap – conditions

Table 5. Spearman's correlations (r_s) between 1985–1986 growth and crown light environment characteristics for *Dipteryx panamensis* and *Lecythis ampla*. $N=10$ for each species

	Diameter growth		Height growth		Leaf area	
	Lecythis	*Dipteryx*	*Lecythis*	*Dipteryx*	*Lecythis*	*Dipteryx*
Total daily PPFD	0.44	0.40	0.68*	0.38	0.45	0.55
Mean % Full Sun	0.55	0.42	0.76*	0.57*	0.48	0.63*
% PPFD as sunflecks	0.49	0.32	0.79*	0.38	–	–
Leaf area	0.21	0.65*	0.82*	0.81*	–	–
Leaf area × mean PPFD	0.41	0.63*	0.90*	0.82*	–	–

* Significant at $P<0.05$

Table 6. Spearman's correlations (r_s) between crown size and crown light environment characteristics for *Dipteryx panamensis* and *Lecythis ampla*. $N=10$ for each species

	Crown area		Crown volume		Height	
	Lecythis	*Dipteryx*	*Lecythis*	*Dipteryx*	*Lecythis*	*Dipteryx*
Total daily PPFD	0.39	0.29	0.50	0.48	0.52	0.33
Mean % Full Sun	0.62*	0.37	0.75*	0.57*	0.64*	0.54
Intra-crown variability (CV of sensor total PPFD)	−0.28	0.73*	−0.28	0.82*	−0.28	0.62*

* Significant at $P<0.05$

(Chazdon and Fetcher 1984), our concepts of gap dependency and regeneration need to be refined. Recent work indicates that in several other aspects, *Dipteryx* does not conform to the characteristics usually ascribed to a gap-dependent species (Clark and Clark 1987a, b).

Although the two species differed significantly in terms of median daily total PPFD, the quantum flux densities and their difference were quite low relative to the full sun value of 30 mole m^{-2} d^{-1} (0.31 mole m^{-2} d^{-1} for *Lecythis* vs 0.42 mole m^{-2} d^{-1} for *Dipteryx*). Nevertheless, as a result of the low PPFD fluxes overall, the difference between these two species is potentially important. More than 90% of the photon flux densities measured in the present study were below 25 μmol m^{-2} s^{-1} which is undoubtedly in the light-limited region of photosynthesis for both of these species. Simulations for understory palms (Chazdon 1986) suggest that when most of the total daily PPFD is comprised of diffuse radiation, the relation between total daily PPFD and total daily carbon gain is linear. Growth and survivorship of a variety of tropical tree seedlings at La Selva was substantially different between treatments of one and two percent of full sun (N. Fetcher, pers. commun.). The finding that saplings of *Dipteryx*, with only one-half the leaf area, had similar height and diameter growth to those of *Lecythis*, supports the importance of the measured difference in incident irradiance and suggests that the species may differ in photosynthetic characteristics as well.

Sunflecks make a significant contribution to the total PPFD received by saplings of these two species. Although the average for both species was between 18–20 min of sunfleck per day, among individual saplings the mean total time of sunflecks per day ranged from 2 to 106 min for *Dipteryx* and 1 to 94 minutes for *Lecythis*. Of the two species, *Lecythis* had the better correlations between growth and the proportion of PPFD from sunflecks. The extent to which sunflecks contribute to the carbon gain of these species will depend on the photosynthetic characteristics of forest grown saplings which at present are unknown.

It is encouraging that short-term light measurements over such a small range of PPFD could produce significant correlations with annual height growth. Pearcy (1983) found significant correlations of sapling growth and light climate with slightly smaller sample sizes, but he used direct site factor from hemispherical photographs. Neither species in the current study showed strong correlations of light environment with diameter growth, an indication that biomass allocation to height rather than diameter growth in an understory environment is more likely to improve the growth status of the plant (Brokaw 1985). Certainly for the growth form of *Dipteryx*, height growth predominates, because there is virtually no lateral branching in saplings less than ca. 4 m tall.

The strength of correlations of light environment with growth depended on which index of light environment was used; growth and crown characteristics were better correlated with percentage of full sun than with weekly total PPFD. By scaling daily sapling total PPFD with the simultaneous full sun PPFD, the effects of short-term weather events that occurred over a measurement interval were reduced. The percentage of full sun is dependent more on the forest canopy structure and less on the stochasticity of the interaction of clouds with solar angle than are actual values of PPFD, and as a result gives a better estimate of relative light environment. However, percentage of full sun is clearly weather dependent; at sites where diffuse light is important, a cloudy day will result in a higher percentage of full sun than a clear day.

The frequent occurrence of maximum irradiances in mid-morning and early afternoon suggests that low-angle, direct beam light is important for these saplings. Openings in the forest canopy need not be directly overhead, that is, in a gap in the traditional sense, to be important for understory saplings. It must kept in mind that because sensors were positioned to estimate the natural light environment within crowns by matching the sensor angles with leaf angles (Gutshick et al. 1985), lateral light contributions to total daily PPFD were enhanced relative to what would have been found with measurements made with horizontal sensors. It is clear that the disproportionately large amount of light from lateral sources is not a consequence of a few saplings located on slopes; mid-morning and mid-afternoon irradiance maxima were found for saplings growing on level sites. Although the influence of afternoon cloud formation could be seen in the pattern of maximum half-hour mean irradiance, morning and mid-afternoon peak irradiances cannot be attributed to weather pattern alone.

Based on the large difference in crown architecture of the two species, we had anticipated that intra-crown variability in irradiance would differ between the two species. Crowns of *Dipteryx* occupy an estimated 50% of the area and 25% of the volume of crowns of *Lecythis*. Although differences were not significant, all measures of intra-crown variability were larger for *Lecythis* than for *Dipteryx*. Furthermore, perhaps in part as a result of the smaller crown size of *Dipteryx*, intra-crown variability was significantly correlated with crown size and sapling height for *Dipteryx* but not for *Lecythis*. It is not clear, however, whether the strength of these correlations is derived from crown and leaf display characteristics that change with plant size or from differences in the variability of incoming PPFD resulting from different inter-sensor distances. Because of the single-meristem growth form of *Dipteryx*, self-shading within the crowns of larger saplings is likely a contributing factor.

The absence of a significant difference between the two species in terms of intra-crown variability was a result of extremely large variability in light environment on a small scale, in space as well as time. The light climate in tropical forest understory has previously been shown to be highly variable on the scale of individual plants (Yoda 1974; Pearcy 1983). In this study we have shown that the variability extends to the level of the individual leaf and leaflet as well. The physiological implications are clear; understory leaves can not be considered a photosynthetically uniform population because differences in intra-crown irradiance during leaf development can lead to differences in photosynthetic characteristics via acclimation. Fetcher et al., unpublished work, in a shadehouse study found that *Dipteryx* exhibits greater adjustments in photosynthetic rate with increases in light during growth than does *Lecythis*. The potential contribution of these differences to whole plant carbon gain is currently under investigation.

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