

Long-term study of solar radiation regimes in a tropical wet forest using quantum sensors and hemispherical photography

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Abstract

Daily photosynthetic photon flux density (PPFD) was monitored for 1 year in the understorey of a tropical wet forest along a transect extending from a treefall gap to the closed canopy at La Selva Biological Station, Costa Rica. Quantum sensors attached to data loggers were operated continuously. Hemispherical photographs were taken monthly above the sensors. An additional quantum sensor was used to monitor PPFD outside the canopy. Sensor measurements show large differences between gap and closed-canopy locations and high daily and seasonal variability at each sensor location, with notable increases in solar radiation in gap stations during September and April. The photographs demonstrate that seasonal variation in PPFD results primarily from shifts in the solar angle relative to canopy openings and secondarily from variation in PPFD levels outside the canopy (cloudiness). Photographs also demonstrate an overall decrease in PPFD with time, for the gap stations, owing to vegetation regrowth. Analyses reveal excellent agreement between sensor PPFD measurements and estimates from hemispherical photographs. Long-term monitoring of PPFD enables calibration of hemispherical photography to permit estimation of PPFD with a high degree of reliability.

Introduction

Solar radiation flux in the understorey of forests is determined by daily and seasonal shifts in solar angle, weather, and the geometry of canopy openings

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as they change with time (Reifsnyder et al., 1971; Reifsnyder, 1989). Wet tropical forests are of considerable interest because they are structurally diverse and dynamic, and few data exist concerning understorey microclimate. In the understorey, solar radiation levels are typically low, and photosynthetically active radiation (PAR) is generally a limiting resource for plants (Percy, 1990; Chazdon and Percy, 1991). Recent attention has focused on the importance of canopy gap dynamics in regeneration and ecosystem processes of tropical forests (e.g. Whitmore, 1975, 1978; Hartshorn 1978; Brokaw, 1985; Denslow, 1987; Clark, 1990; Lawton, 1990; Canham et al., 1990). Though many studies have examined disturbance regimes and species' responses to canopy gaps, relatively few studies have focused on solar radiation, and these have generally involved short-term monitoring to determine variability at time scales of seconds to days (e.g. Percy, 1983; Chazdon and Fetcher, 1984; Chazdon and Field, 1987a); with the exception of Brown (1990), no previous study has monitored understorey solar radiation continuously throughout an entire year in a tropical wet forest to determine variability at time scales of days to months.

The development of multi-channel data loggers and use of inexpensive gallium arsenide phosphide photodiodes for quantum sensors greatly expands possibilities for the long-term study of solar radiation flux (Gutschick et al., 1985; Oberbauer et al., 1989). However, long-term studies with quantum sensors are still limited to relatively few sampling locations both because of expense and effort. Furthermore, site characterization by short-term measurements is of questionable value because of high variability; and individual quantum sensors cannot spatially resolve relations between canopy geometry and solar radiation flux. Used in conjunction with hemispherical photography, these limitations can be overcome. Hemispherical photography, which involves taking photographs looking upward from beneath a canopy through a 180° lens, permits direct measurement of the geometry of canopy openings and estimation of solar radiation flux (Evans and Coombe, 1959; Anderson, 1964; Percy, 1989; Rich, 1990). Recently developed systems for semi-automated image analysis of hemispherical photography present the means to analyze large numbers of photographs (Chazdon and Field, 1987b; Rich, 1988, 1989; Becker et al., 1989). Various studies have shown good correspondence between sensor measurements and photograph calculations of photosynthetic photon flux density (PPFD) for periods ranging from minutes to weeks (e.g. Chazdon and Field, 1987b; Becker et al., 1989).

Here we examine temporal variability of solar radiation over the course of an entire year using quantum sensors and hemispherical photographs. The primary goal is to understand the variation in solar regimes that results from both deterministic and stochastic processes. Though the field study was conducted in a tropical wet forest, where the sun is close to the zenith at noon and foliage is dense, the findings can be generalized to include both tropical

and temperate systems. First, we characterize temporal variability of solar radiation in a treefall gap and in a closed-canopy understorey. Second, we distinguish the importance of seasonal shifts in solar angle, changes in solar radiation levels outside the canopy, and changes in canopy geometry (formation and closure of gaps) for solar radiation penetration into the understorey. Finally, we investigate the agreement between sensor measurements and photograph estimation of photosynthetic photon flux density (PPFD).

Methods

Study site

The study site was in the understorey of a small gap and adjacent closed-canopy locations in primary tropical wet forest at the Organization for Tropical Studies', La Selva Biological Station, Costa Rica (10°26' N, 32°59' W, 35 m elevation) (see Holdridge et al., 1971; Hartshorn, 1983 for further site descriptions). We selected this gap because it was accessible and close to the median gap size at La Selva (median gap size = 110 m², Sanford et al., 1986). The study gap measured approximately 94 m² (vertical projected area clear from > 2 m above the ground to the sky, see Brokaw, 1985), with a 15 m long major axis oriented approximately east–west (along a 75–255° azimuth) and a 10 m long minor axis. Seven sample stations were established within the gap and nearby closed-canopy forest. Stations 1, 2 and 3 were located along the major axis across the gap center and Station 4 was along the west edge of the opening. The closed-canopy Stations 5, 6 and 7 were sited along the same east–west axis in mature-phase forest, with no understorey vegetation from ground level to at least 3 m. These were on flat ground, while the gap stations sloped approximately 10° from Stations 4 to 1. Distances between sequential stations, from 1 to 7, were 3 m, 4 m, 4 m, 5 m, 10 m and 7 m respectively. An additional sample station was established in an open field approximately 800 m from the forest site to monitor PPFD outside the canopy (hereafter referred to as 'above-canopy').

PPFD measurements with solar radiation sensors

PPFD was measured daily from 6 May 1987 until 17 May 1988. In the forest, PPFD was measured using gallium arsenide phosphide photodiodes (Hamamatsu G1118, Hamamatsu, Middlesex, NJ) calibrated against a Li-Cor Li-190 quantum sensor (Li-Cor, Lincoln, NE). Low-cost gallium arsenide phosphide sensors have good quantum response, with sharp cutoffs near 400 and 700 nm (Gutschick et al., 1985; Chazdon and Field, 1987b; Oberbauer et al., 1988). Measurements were taken every 10 s, stored as 30 min averages on data loggers (Campbell Scientific CR-21, Campbell Scientific, Logan, UT),

written to audio cassette tapes, and used to calculate daily totals (see Oberbauer et al., 1988, 1989 for further details). The sensors were mounted on 9 cm × 9 cm posts at 1.3 m above the ground. A removable plastic sensor mount was secured by four corner pins to insure constant positioning. Above-canopy PPF_D was measured using a Li-Cor Li-190 quantum sensor. Sensors were checked daily both physically and via the data logger. Every 1–3 months the transect sensors were brought to the laboratory and recalibrated against a Li-Cor Li-190 quantum sensor.

Problems with the sensors, data loggers, and tape recorders resulted in various days for which data are missing from at least one of the transect positions or the abovecanopy station. We calculated summary statistics of monthly PPF_D for the seven forest stations and the above-canopy station (means, ranges, and coefficients of variance) using all the data available for each station during that period (mean $n = 25$ days/month, range 11–31 days/month). For statistics of daily PPF_D values, we used only the subset of days for which there were usable data at all stations simultaneously ($n = 258$ days). We calculated Pearson's correlation coefficients to determine relations on a daily basis between forest understory station PPF_D, above-canopy PPF_D, and rainfall.

Characterization of solar radiation regime with hemispherical photographs

Hemispherical (fisheye) photographs were taken above the sensors each month with Kodak Tri-X film (400 ASA, Eastman Kodak, Rochester, NY) using a Nikkor 8 mm hemispherical lens, a Nikon FM2 camera, and a Nikon MF16 databack (Nikon, Melville, NY); exposures were determined with the internal camera sensor (see Rich, 1989). For each photograph, the sensors were removed and the camera was placed on the wooden posts using a self-leveling mount oriented by four corner pins. This insured constant positioning of the camera from photograph to photograph. The top of the lens was 1.5 m above the ground. The camera was oriented such that magnetic north was always located at the top of photographs, to facilitate overlay of the sun track during analysis. When possible, photographs were taken under overcast sky conditions to ensure even backlighting. Starting with the December 1987 photographs, we used a red filter to enhance contrast between openings and adjacent vegetation.

Photographs were analyzed using the video image analysis program CANOPY (Rich, 1988, 1989, 1990). The system allows video digitization of backlit negatives, correction for lens distortion and magnetic declination, interactive determination of a threshold grey level to distinguish openings from foliage, and calculation of direct and diffuse site factors. Direct and diffuse site factors refer respectively to photographic estimations of the pro-

portion of direct and diffuse radiation levels under a canopy relative to the levels outside the canopy (Anderson, 1964).

The CANOPY video image analysis system is based on an IBM-compatible microcomputer equipped with a mathematics coprocessor, an Imaging Technology PCVISIONplus video digitizer/display adapter with an external synchronization cable (Imaging Technology, Bedford, MA), and a Sony PVM1271Q analog RGB monitor (Sony of America, Teanect, NJ). Negatives are backlit using an Aristo V-56 lamp fitted with a 7452 standard color lamp (Marron Carrell, Phoenix, AZ) and positioned precisely using a Marron Carrell positioner compound with a 35 mm negative carrier (Aristo Grid Lamp Products, Port Washington, NY) suspended on a custom stand fitted with optical leveling feet. Images are input through a Cohu 4815-2100 solid-state black-and-white video camera (Cohu, San Diego, CA) fitted with Nikkor 55 mm Micro lens attached with an F to C mount adapter and supported at an appropriate distance from the film positioner using a copy stand. The video signal is flash digitized (30 frames s^{-1}) at a resolution of $512 \text{ (h)} \times 480 \text{ (v)}$ pixels, with seven bits (127 grey levels) of intensity data per pixel. Positive images are displayed on the RGB monitor in real time using the built in lookup table capabilities of the PCVISIONplus adapter. Graphics overlay of an alignment grid on the displayed images allows precise adjustment of size, focus, x and y translation, and rotation, including a correction for magnetic declination. Image classification uses a threshold intensity value, above which pixel values are classified as foliage and below which as openings. This is accomplished by using lookup tables to toggle back and forth between the positive continuous tone image and the classified image, while adjusting a threshold value up and down until the edges of openings in the classified image best match edges observed in the continuous tone image. Threshold determination involves subjectivity, however, practiced operators can achieve a high degree of repeatability (Rich, 1990; Galo et al., 1992; Lin et al., 1992).

Calculations in CANOPY use a highly optimized image combination algorithm (Rich, 1989), in which the classified threshold image is combined with precalculated images of the angular distribution of direct and diffuse components of solar radiation and weighted by factors that can account for atmosphere corrections and cosine correction. These precalculated images serve as pixel-by-pixel lookup tables that enable rapid calculation of the number of pixels classified as openings versus foliage in each sky direction. Direct radiation distribution files specify 168 sets of sky directions, which in our calculations correspond to 30 min intervals through the day and month intervals through the year. Diffuse radiation distribution files specify 160 ranges of sky directions that correspond to 20 ranges of zenith angle and eight ranges of azimuth angle. Both direct and diffuse distributions were calculated to include a correction for radially symmetric lens distortion. For the direct site factor our calculations used weightings for clear-sky conditions and

correction for the path length of the atmosphere as a function of zenith angle at sea level (Rich, 1989). For the diffuse site factor we used weightings for uniform distribution of diffuse skylight as a function of angular direction (Rich, 1989). Thus the diffuse site factor corresponds to angular openness or 'sky view factor'.

For each photograph, we calculated yearly direct and diffuse site factors and monthly direct site factors. No photographs were taken for Station 4 in July 1987 and for all stations in April 1988, so site factors were calculated using mean values from photographs of adjacent months. Estimated site factors for these missing photographs are shown in graphical presentations, but were excluded from statistical analyses. Photographs were analyzed by two operators, after determining that analysis accuracy and reproducibility did not differ significantly between operators. For 14 standard photograph analyses, mean absolute difference for direct site factor between operators (0.006) was less than the mean absolute difference for consecutive analyses of the first operator (0.009).

We compared descriptive statistics (mean, standard error of the mean, median, and range) for yearly site factors ($n = 12$ for all stations except $n = 11$ for Station 4). Monthly direct site factors calculated from the photograph corresponding to each month were examined to identify differences between the forest sample stations, periodic patterns related to sun angle, and directional changes with time. We tested the ability to predict monthly changes in direct site factors from single photographs by comparing yearly courses of monthly direct site factors calculated from photographs taken at the beginning, middle, and end of the study (May 1987, December 1987, and May 1988).

Estimation of PPF_D from hemispherical photographs

We estimated PPF_D on a monthly basis for each photograph using four variations on a simple model that separately accounts for direct and diffuse radiation components (Anderson, 1964; Rich, 1989). The goal was to test the necessity of measuring above-canopy PPF_D and taking photographs at monthly versus yearly scales. In all cases diffuse site factor was calculated assuming a uniform distribution of diffuse radiation as a function of sky direction. The design is summarized as follows:

Model 1: Monthly direct site factors from monthly photographs, above-canopy from yearly average PPF_D.

Model 2: Monthly direct site factors from monthly photographs, above-canopy from monthly average PPF_D.

Model 3: Monthly direct site factor as weighted mean of endpoint photographs, above-canopy from yearly average PPF_D.

Model 4: Monthly direct site factor as weighted mean of endpoint photographs (May 1987 and May 1988), above-canopy from monthly average PPF_D.

Models 1 and 2 use the monthly direct site factor calculated from the photograph of the month being examined (May 1987 through May 1988). For example, at a given station a photograph taken in December 1987 would be used to calculate the December direct site factor. Models 3 and 4 calculate monthly direct site factors as a linearly weighted average of direct site factors from photographs taken at the beginning and end of our period of study. For example, at a given station the December direct site factor is calculated as 5/12 times the December direct site factor calculated from the May 1987 photograph and 7/12 times the December direct site factor calculated from the May 1988 photograph. In this example, the weightings are obtained as a linear function of the time since the first photograph (7 months), the time before the last photograph (5 months), and the total time between endpoint photographs (12 months). Such a linear weighting assumes a linear rate of change in the geometry of canopy openings over time.

Under all models, we define a global site factor (G) that represents the proportion of solar radiation, in our case PPF_D, under a canopy relative to that outside the canopy

$$G = p_{\text{dif}} T_{\text{dif}} + p_{\text{dir}} T_{\text{dir}} \quad (1)$$

where p_{dif} is the proportion of total radiation that is diffuse, T_{dif} is the diffuse site factor (proportion diffuse PPF_D under the canopy relative to that outside the canopy), p_{dir} is the proportion total radiation that is direct ($= 1 - p_{\text{dif}}$), and T_{dir} is the direct site factor (proportion direct PPF_D under the canopy relative to that outside the canopy). The PPF_D (P) is then calculated as a simple product of the above-canopy PPF_D (S) and G

$$P = SG \quad (2)$$

The model can be applied over any time scale; however, all parameters must be formulated at the same time scale. For example the p_{dif} and S for an instantaneous T_{dif} are likely to be very different than for a yearly T_{dif} .

Values used for p_{dif} can be empirically determined or estimated (Becker, 1987); however, no values are currently available for La Selva. In the absence of empirically determined values, various researchers have assumed p_{dif} ranging from 0.15 (Chazdon and Field, 1987b) to 0.5 (Canham et al., 1990), formulated on the basis of simple models and published atmospheric transmission coefficients. Rather than assume a single value, for our models we vary p_{dif} between 0.0 and 1.0 and examine effects on the regression of observed PPF_D against estimated PPF_D. These models only account for solar radiation that enters directly through canopy openings, and ignore scattered radiation that is transmitted through or reflected downward from leaves.

Table 1
Summary of mean PPFD for month periods from May 1987 through May 1988

Station	Mean PPFD Mols m ⁻² day ⁻¹	Mean percent above-canopy PPFD	Mean CV
1	2.50 (1.1–4.9)	9.2 (3.8–17.1)	48.9
2	2.94 (0.9–6.8)	10.6 (3.5–21.4)	49.9
3	2.47 (0.8–5.5)	9.0 (3.1–17.3)	46.5
4	2.77 (0.9–5.1)	10.1 (3.6–17.3)	44.2
5	0.44 (0.2–1.2)	1.6 (0.6–4.1)	50.6
6	0.42 (0.2–0.9)	1.5 (0.8–2.9)	38.2
7	0.35 (0.2–0.5)	1.3 (0.6–1.8)	44.7
Above-canopy	27.41 (23.6–31.8)	–	35.1

Percent values are relative to the monthly above-canopy PPFD. Values in parentheses are the ranges of monthly means. Mean CV is the average of coefficient of variation of monthly means. Stations 1 through 4 were in the gap, Stations 5 through 7 were under closed canopy.

To evaluate the utility of each model, we examined suites of regressions of observed PPFD against estimated PPFD in which we varied p_{dif} from 0.0 to 1.0. We plotted the r^2 , slope and intercept as a function of p_{dif} to determine the best estimations of PPFD.

Results

PPFD sensor results

Over the 1-year period, the gap stations (1–4) were very similar, averaging 9–11% of the mean above-canopy PPFD (Table 1). Station 4, which was selected to be a gap edge station, in fact was indistinguishable from the other gap stations. The closed canopy stations (5–7) were also very similar, averaging less than 2% of the above-canopy mean.

Between months there were pronounced differences as well as strong temporal patterns (Fig. 1). Mean PPFD varied from month to month by a factor of three to seven at each station. Coefficients of variation of monthly data were similar at gap and understory stations; above-canopy variation was lower (Table 1). Monthly means were positively, but not significantly, correlated with above-canopy monthly means at all seven stations; six of seven correlations with monthly rainfall were negative, but only one was significant. When the monthly means are expressed as percents of the above-canopy monthly means, all of the gap stations varied more than 13% among months, while understory stations varied 1–3%.

Above-canopy monthly mean PPFD was highest in April and lowest in July and August (Fig. 1(a)). The gap stations show pronounced peaks in September and April; the April peak is higher than the September peak for Stations 2, 3, and 4, but lower for station 1 (Fig. 1(b)). Closed-canopy Station 5

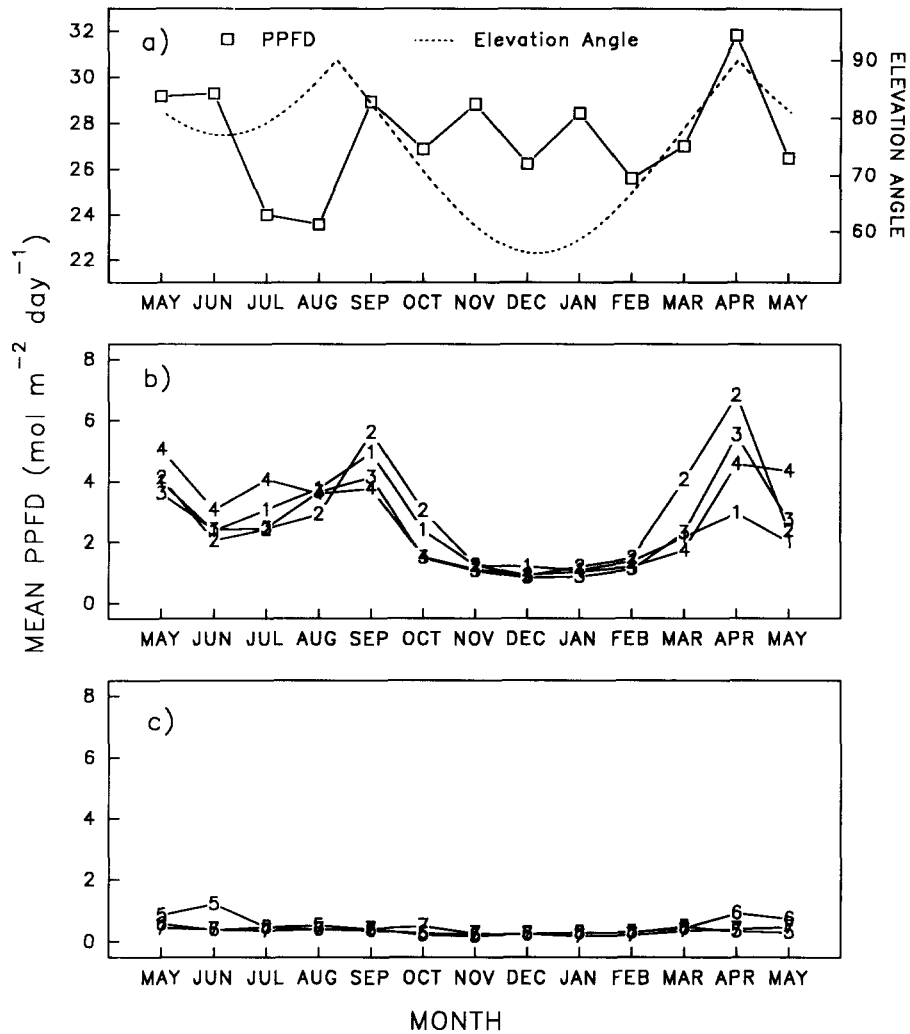


Fig. 1. Seasonal changes in mean monthly photosynthetic photon flux density (PPFD) (solid line) and solar elevation angle at noon (dashed line) from May 1987 to May 1988 for (a) above-canopy station, (b) gap Stations 1 through 4, and (c) closed-canopy Stations 5, 6, and 7. Numbers in each curve correspond to sample stations.

experienced a month-long period of approximately double the PPFD of the other closed-canopy stations during June 1987 and Station 6 experienced a similar period in April 1988 (Fig. 1(c)). The gap stations showed a precipitous decrease in PPFD in October 1987, which lasted until March 1988. This prolonged depression was not due to a decrease in the above-canopy PPFD (Fig. 1(a)).

There was substantial daily, monthly, and seasonal variance in PPFD at

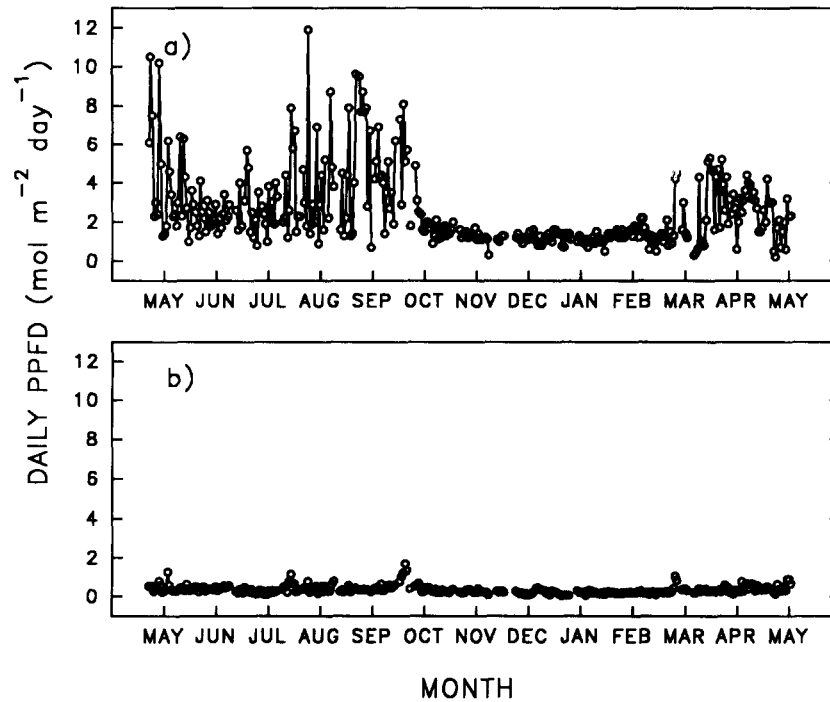


Fig. 2. Daily total PPFD from May 1987 to May 1988 for (a) Station 1 and (b) Station 7.

each station. Between consecutive days, daily means commonly changed two to four-fold (Fig. 2). Most daily variation at each sensor was not explained either by variation in rainfall or above-canopy PPFD (Table 2). The maximum r^2 between the daily PPFD for any station with above-canopy

Table 2

Pearson's correlation coefficients between total daily PPFD for the forest gap stations (ST1 through ST4), the closed-canopy stations (ST6 through ST7), the total daily PPFD for the above-canopy station (AC), and total 24-h rainfall (RAIN)

	ST1	ST2	ST3	ST4	ST5	ST6	ST7	AC
ST2	0.74**							
ST3	0.79**	0.88**						
ST4	0.68**	0.66**	0.83**					
ST5	0.31**	0.22**	0.31**	0.44**				
ST6	0.40**	0.57**	0.65**	0.70**	0.24**			
ST7	0.50**	0.43**	0.44**	0.51**	0.30**	0.44**		
AC	0.50**	0.51**	0.49**	0.50**	0.39**	0.48**	0.38**	
RAIN	-0.11	-0.24**	-0.17**	-0.15*	-0.13*	-0.20**	-0.17**	-0.43**

Only days for which data for all variables were measured are included ($n = 258$). * = $p < 0.05$, ** = $p < 0.01$.

Table 3

Descriptive statistics of site factor calculations for hemispherical photographs taken on consecutive months from May 1987 to May 1988 (except April 1988; data for July 1987 Station 4 were lost)

SITE FACTOR	STATION	MEAN	SEM	<i>n</i>	MED	MIN	MAX
<i>Diffuse</i>	1	0.076	0.0057	12	0.075	0.043	0.104
	2	0.086	0.0056	12	0.082	0.061	0.118
	3	0.079	0.0047	12	0.079	0.054	0.108
	4	0.082	0.0064	11	0.079	0.055	0.111
	5	0.026	0.0051	12	0.019	0.009	0.063
	6	0.029	0.0030	12	0.030	0.011	0.049
	7	0.031	0.0037	12	0.035	0.005	0.047
<i>Direct</i>	1	0.080	0.0059	12	0.079	0.046	0.111
	2	0.084	0.0066	12	0.080	0.054	0.124
	3	0.073	0.0051	12	0.071	0.049	0.110
	4	0.092	0.0062	11	0.092	0.063	0.113
	5	0.023	0.0039	12	0.015	0.008	0.047
	6	0.026	0.0031	12	0.025	0.014	0.050
	7	0.027	0.0031	12	0.026	0.005	0.044

SEM is standard error of the mean, MED is median, MIN is minimum, and MAX is maximum.

values was only 0.26, and the r^2 between PPF and rainfall was even lower, 0.06. Among the stations, daily PPF values for the gap stations were more correlated among themselves (Table 2, r range 0.68–0.88) than were the understory stations (r range 0.24–0.44).

Hemispherical photography results

Yearly estimates of direct and diffuse site factors varied relatively little among months at each station (Table 3). As for PPF, site factors were similar among gap Stations 1 through 4 and among closed-canopy Stations 5 through 7, and were different between gap and closed-canopy stations. Monthly direct site factors calculated from each month's photographs differed between gap and closed-canopy stations (Fig. 3). For gap stations, peaks were expected for August and April, the same months for which the solar elevation angle is highest at noon (Fig. 1(a)). Though the April peaks in direct site factors for the gap stations correspond with the measured April peaks in PPF, the August peaks are a month before the PPF September peak, and are coincidental with the lowest monthly above-canopy PPF. For the closed-canopy stations, there is a decrease in monthly direct site factor with time, with a slight rise in the last months.

Monthly direct site factor calculated from single photographs show similar seasonal patterns, with peaks in August and April for gap stations; however, amplitude decreases markedly for calculations using May 1987, December 1987, and May 1988 photographs (Fig. 4). The sequential hemispherical photographs for each sample station demonstrate gap closure (Fig. 5).

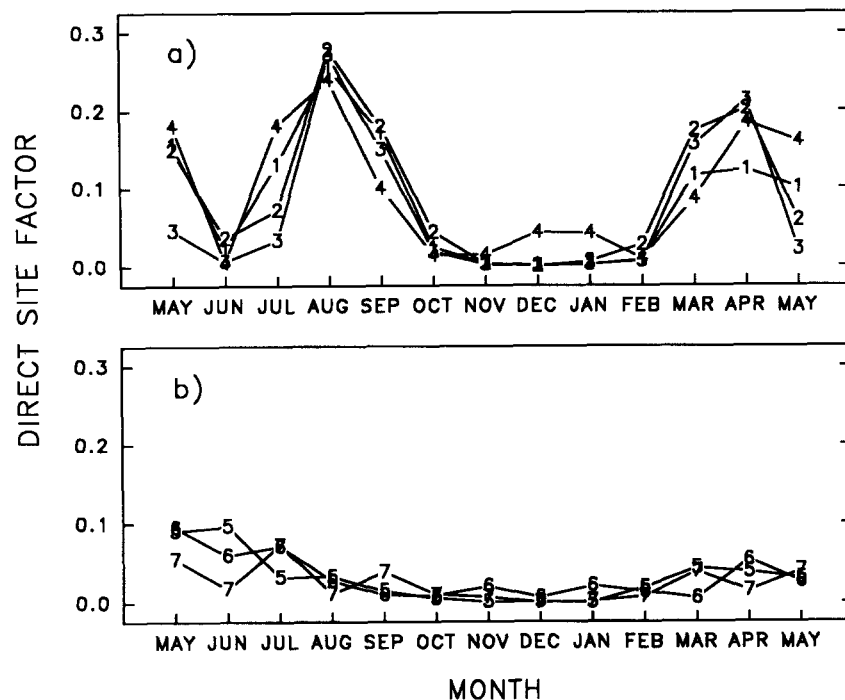


Fig. 3. Monthly direct site factors calculated from monthly hemispherical photographs for (a) gap Stations 1 through 4 and (b) closed-canopy Stations 5, 6, and 7.

Models 1, 2, 3, and 4 all yield good estimates of PPFD from hemispherical photographs, with maximum r^2 values between 0.7 and 0.8 (Fig. 6(a)). Values of r^2 are greatest with intermediate weighting of diffuse site factor ($p_{\text{dif}} = 0.75$ for Models 1 and 2 and $p_{\text{dif}} = 0.55$ for Models 3 and 4). The maximum r^2 values all give slopes near 1 and intercepts near 0 (Figs. 6(b), 6(c)). Inclusion of above-canopy monthly PPFD improves r^2 , especially between Models 3 and 4. To a lesser degree, use of all monthly photographs also increases r^2 . As a typical example of model results, Fig. 7 shows an excellent match between sensor measurements and photographic estimations of monthly PPFD using Model 4.

Discussion

Rather than observing a gradient of solar radiation environments from the gap into closed-canopy understorey sample stations, we observed two distinct groups, gap and closed-canopy (Table 1, Fig. 1). Similarity of PPFD measurements for the gap stations resulted because the stations were situated along an east–west transect. Direct sunlight penetrated for similar durations, though during different periods through the day, because similar proportions of sky

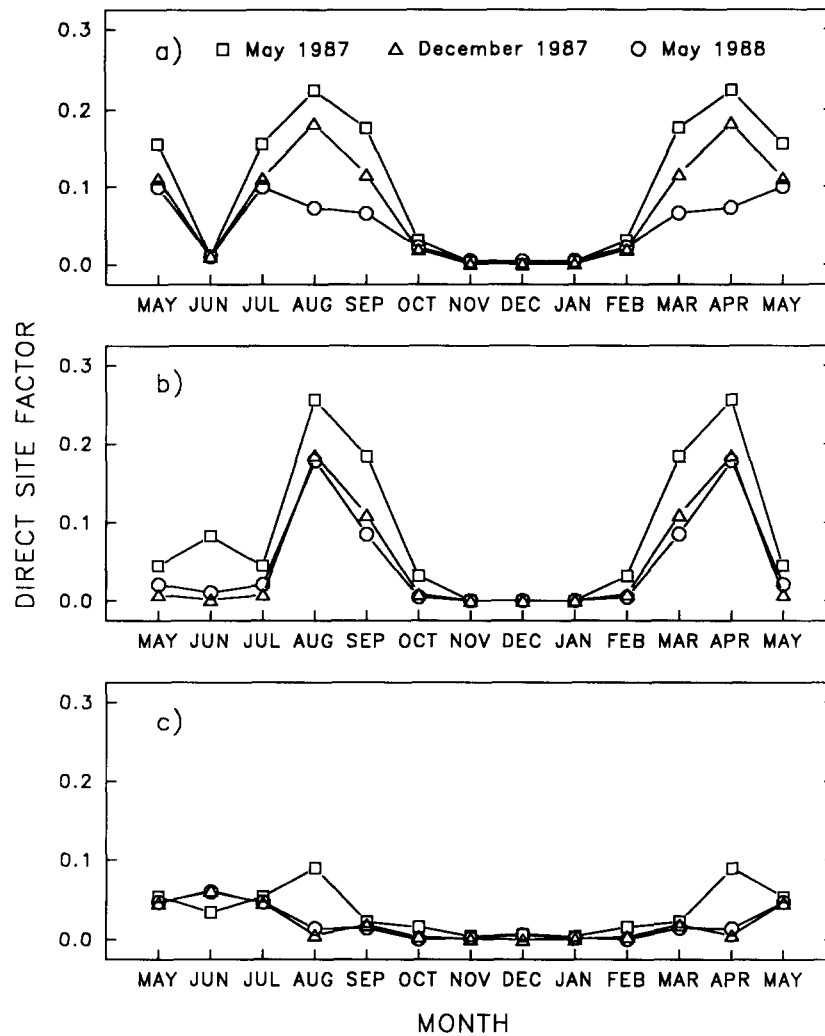


Fig. 4. Monthly direct site factors calculated from single photographs in May 1987, December 1987, and May 1988 for (a) Station 1, (b) Station 3, and (c) Station 7.

were unobscured along the sun track. Such a result is likely to be most pronounced near the equator, where the sun track goes nearly east–west and crosses near the zenith during much of the year. This result may not be generalizable if afternoons tend to be cloudier than mornings at La Selva, such that the west side of gaps might be expected to receive more solar radiation than the east side. The similarity of the closed-canopy stations resulted from similar degrees of canopy closure. In all cases we found high variation, both among months (Fig. 1) and days (Fig. 2).

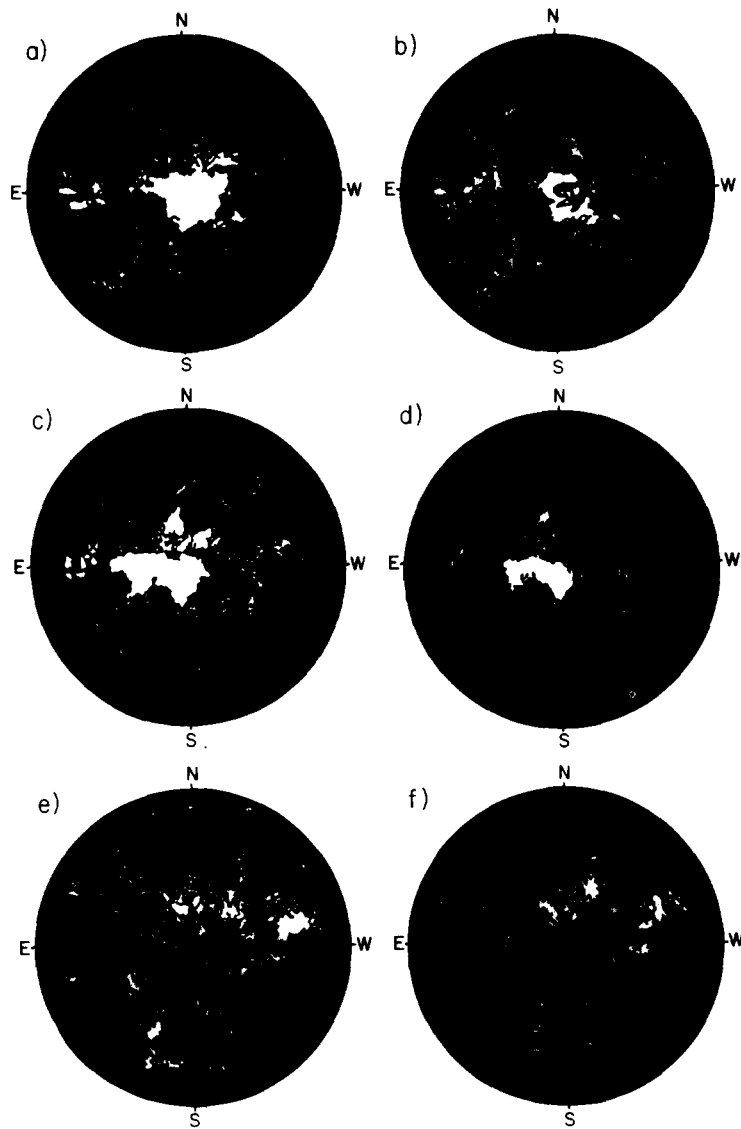


Fig. 5. The pattern of canopy openings in hemispherical photographs taken for (a) Station 1 in May 1987 (diffuse site factor = 0.104, direct site factor = 0.107), (b) Station 1 in May 1988 (diffuse site factor = 0.043, direct site factor = 0.045), (c) Station 3 in May 1987 (diffuse site factor = 0.110, direct site factor = 0.101), (d) Station 3 in May 1988 (diffuse site factor = 0.054, direct site factor = 0.049), (e) Station 7 in May 1987 (diffuse site factor = 0.034, direct site factor = 0.031), and (f) Station 7 in May 1988 (diffuse site factor = 0.025, direct site factor = 0.019). Both Stations 1 and 3 showed marked gap closure. Note that east and west are reversed because photographs are taken looking upward.

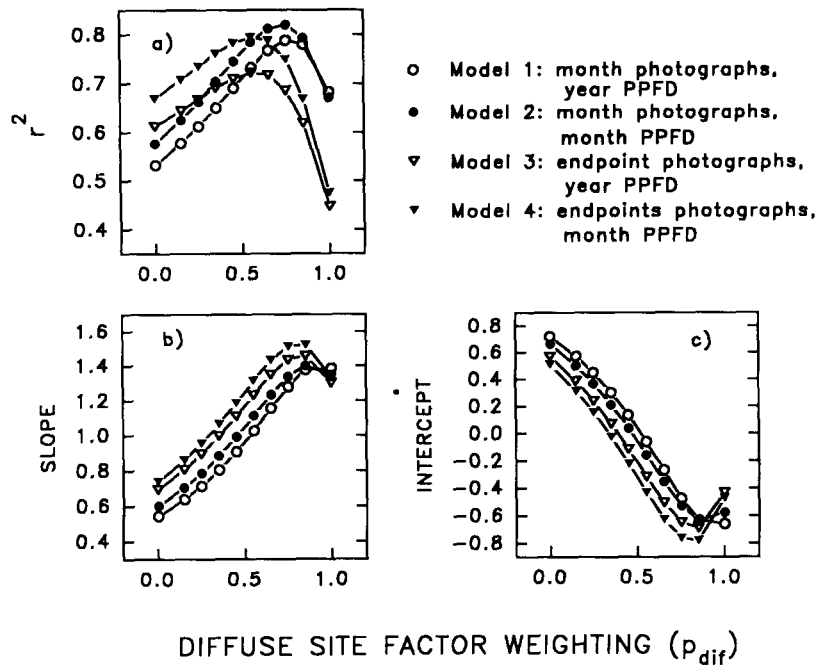


Fig. 6. Regression statistics (a) r^2 , (b) slope, and (c) intercept as a function of the diffuse site factor weighting (p_{dif}) for each of four PPF estimation models tested. All regressions are of monthly calculated PPF at each site against observed monthly mean PPF (seven stations \times 13 months = 91 points).

Caution must be exercised when reporting radiation flux as a proportion of above-canopy PPF, because different results are obtained depending upon whether instantaneous, daily, monthly, or yearly above-canopy PPF is used as the reference. Our proportional PPF values (Table 1) are not directly comparable with instantaneous measurements, for instance standardized to be taken only near noon on a clear day. Such instantaneous indices do not integrate shifts in solar angle through the day or variation in above-canopy conditions. In addition, any index based on short-term measurements at a particular time of the year is subject to major variation resulting from seasonal shifts in solar angle.

We found only a weak correlation between daily above-canopy PPF and PPF for the closed-canopy sample stations (Table 2). The effects of short-term fluctuations in above-canopy PPF can be important only if they coincide with times when the sun can directly penetrate through canopy openings. A day with high above-canopy PPF may not have high PPF beneath the canopy if clouds obscure the sun at times when direct penetration could occur. Likewise, brief absences of clouds when the sun lines up with canopy openings can lead to high understorey PPF on days with low above-canopy PPF. We also found only a weak negative correlation

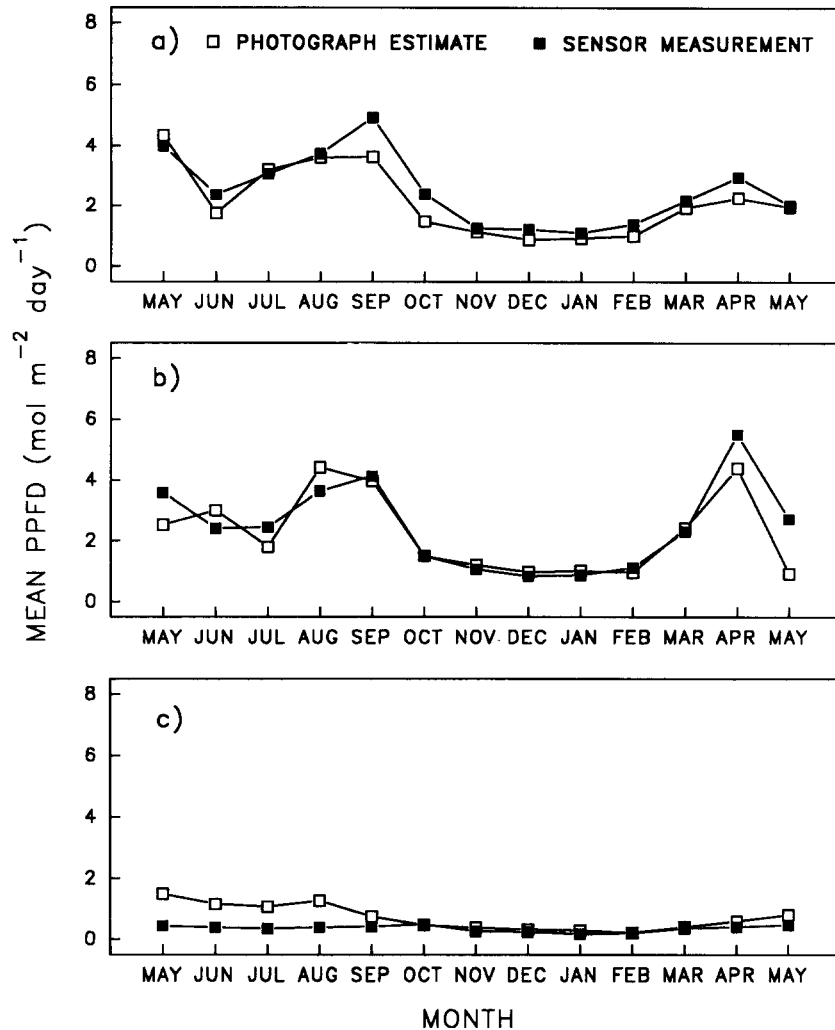


Fig. 7. A sample of correspondence between calculated and observed mean PPFD using Model 4, with monthly direct site factors calculated as linearly weighted averages of monthly direct site factors from May 1987 and May 1988 hemispherical photographs and weighted by the monthly mean above-canopy PPFD for (a) Station 1, (b) Station 3, and (c) Station 7. The value $p_{\text{dif}} = 0.55$ ($r^2 = 0.794$) was used for the diffuse site factor weighting and a slope of 1.32 and intercept of -0.43 were used to calibrate the calculations to observed values.

between daily rainfall and PPFD for the forest sample stations (Table 2). This results, in part, because rainfall is only a weak predictor of cloudiness, and, in part, because of the same timing considerations wherein clouds may accompany rainfall at times when the sun does not line up with canopy openings.

From the sensor data alone, it is not possible to deduce causes of variation

in monthly PPF_D. The patterns of PPF_D peaks and troughs measured for the gap stations do not result simply from increases or decreases in above-canopy PPF_D (Fig. 1). Though high above-canopy PPF_D for April coincides with PPF_D peaks for the gap stations, no other correspondence is apparent. The April PPF_D levels are higher than the September PPF_D levels for Stations 2, 3, and 4, but lower for Station 1. On the basis of sensor measurements alone, it might be postulated that the September and April PPF_D peaks (and the November through February PPF_D trough) could result from seasonal changes in solar angle. One can further postulate that the canopy above Station 1 has closed in. However, these conjectures can only be verified by more direct measures of canopy geometry, such as hemispherical photography.

Effects of seasonal shifts in solar angle and gap closure are apparent from analyses of hemispherical photographs. Peaks of direct sunlight penetration for the gap stations are expected for August and April; months which are symmetrical about the summer solstice (Figs. 3 and 4); and the gap is observed to close dramatically (Fig. 5). In the case of this small gap, closure results from growth of trees from the sides of the gap, rather than by marked growth from the understorey. Station 1 shows the greatest closure, because of growth by a tree about half way to the canopy top. The direct site factor values are not calibrated to include seasonal differences in above-canopy PPF_D. On the basis of these analyses, PPF_D peaks are expected in August, rather than September as observed with the sensors; and the April PPF_D peaks are expected to be smaller because of gap closure, with the decrease most pronounced for Station 1.

The combined use of PAR sensors and hemispherical photography allows us to discern the relative importance of solar radiation levels outside the canopy, seasonal shifts in solar angle, and changes in the geometry of canopy openings with time for radiation penetration into the plant canopy. The August peak expected from the photograph analyses alone does not occur because of low above-canopy PPF_D during August, but rather is shifted to September, when higher above-canopy PPF_D coincides with angles favorable for direct radiation penetration. Even though the gap decreased in size, Stations 2, 3, and 4 display the highest monthly PPF_D during April because of high above-canopy PPF_D and coincidence between midday solar angles and the canopy openings during April. Because gap closure for Station 1 was most pronounced, April PPF_D peaked at a lower level than for the other gap stations. All four models for estimation of PPF_D from hemispherical photographs are consistent with this interpretation.

Among the models, inclusion of above-canopy PPF_D weightings (Models 2 and 4) improves the r^2 considerably (Fig. 6). Though slightly higher r^2 values were obtained by using direct site factors from photographs taken every month (Models 1 and 2), the improvement over linear interpolations between

endpoint photographs was very slight in comparison to Model 4. This suggests that the optimal sampling scheme requires continual monitoring of above-canopy PPFD. However, at least for the directional gap closure we observed over the course of 1 year, interpolations from endpoint photographs are sufficient. A linear calibration can be used to translate global site factor (calculated from direct and diffuse site factors) to PPFD. The relative proportions of direct and diffuse site factors used to calculate global site factor can be estimated from atmospheric clarity (Becker, 1987; Canham et al., 1990), obtained empirically (Becker, 1987; Becker et al., 1989), or calculated by locating the optimum r^2 as a function of different weightings, as demonstrated by our results (Fig. 6). The latter, as used for this study, is a best fit model, whereas the former are more mechanistic models.

An empirical calibration allows refined prediction of PPFD from hemispherical photographs. Such calibration does not affect the ability to make relative comparison between photographs. In the absence of any long-term monitoring of PPFD with sensors, hemispherical photographs still allow meaningful microsite comparison. For between site comparisons, it is useful to report both direct and diffuse site factors and calculations of PPFD. We monitored PPFD over only a limited range of forest solar radiation conditions, so our calibrations are only verified for a range from about 1 to 10% relative to daily above-canopy PPFD. Estimation of PPFD from hemispherical photographs appears to be robust, so more general use of our calibrations is probably warranted. Calibrations are particular to the forest site, time of year, and range of pattern of canopy openings observed.

Hemispherical photography has been used successfully in a broad range of studies involving microsite characterization of solar radiation regimes (e.g. Turton, 1988; Turner, 1990; Becker et al., 1990; Canham et al., 1990; Weiss et al., 1991; Galo et al., 1992; Lin et al., 1992). Meaningful results can only be obtained by strict quality control: (1) to acquire high contrast, evenly backlit photographs with no reflections off leaves; and (2) to standardize results obtained from different operators. Three directions are desirable for future development of methodology: first, improving the means for distinguishing foliage from openings, second, further incorporating site-specific measurements concerning the angular distribution of direct and diffuse above-canopy PPFD, and third, incorporating canopy penumbral and scattering properties in the models to calculate PPFD.

Both the sensor and photographic techniques have distinct strengths and limitations. Used together, it is possible to discern causes of temporal variation in solar radiation. While sensors offer direct measurement of PPFD, photographs allow direct measurement of canopy geometry and indirect prediction of PPFD. High PPFD variability between days and months makes it difficult to characterize microsites on the basis of short-term PAR sensor measurements. Hemispherical photographs can not substitute for sensor

measurements in studies of such processes as photosynthetic carbon balance, sunfleck dynamics, and photoinhibition. However, because long-term monitoring with sensors is generally not practical or economically feasible, and because only a few microsites can reasonably be studied in detail, hemispherical photographs can greatly enhance the number of microsites for which solar radiation regimes can be characterized.

Conclusion

Long-term monitoring of solar radiation under plant canopies reveals the difficulty of characterizing solar radiation microclimate on the basis of short-term measurements for a limited number of sample locations. Our 1-year study of solar radiation regimes in gap and closed-canopy understorey sites represents the longest sampling of PPFD under tropical wet forest canopies to date. The combined use of PAR sensors and hemispherical photography enabled accurate characterization of microsites and mechanistic understanding of the causes of temporal radiation variability. At day to year scales, we were able to distinguish variability resulting from seasonal shifts in solar angle, changes in radiation levels outside the canopy, and changes in the geometry of canopy openings. Simple models allow estimation of PPFD from hemispherical photographs. Accurate estimation of PPFD is best accomplished by calibrating photographic measurements with long-term sensor measurements.

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