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PHOTOSYNTHETIC LIGHT ENVIRONMENTS IN A LOWLAND TROPICAL RAIN FOREST IN COSTA RICA

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SUMMARY

(1) Measurements of photosynthetic photon flux density (PPFD) in four sites within a lowland tropical rain forest were compared. The habitats investigated were a 0·5 ha clearing, a 400 m^2 gap, a 200 m^2 gap, and heavily shaded understorey.

(2) Measurements were made during both wet and dry seasons under a variety of weather conditions. Quantum sensors were used to monitor continuously 10-min average PPFD over a 3–10 day period at each location. Daily average PPFD, total daily PPFD, and daily frequency distributions were analysed for two adjacent sensors per site on each sampling day.

(3) Daily total PPFD in the understorey, 200 m^2 gap, and 400 m^2 gap were 1–2%, 9%, and 20–35%, respectively, of PPFD in the clearing. Daily total PPFD in the 400 m^2 gap during the dry season was, on average, 2·4 times greater than in the 200 m^2 gap, and 20–25 times those in the understorey. In the 200 m^2 gap, daily total PPFD was nine times greater than in the understorey during the dry season.

(4) In the clearing, PPFD was significantly different between seasons with 24% higher PPFD during the dry season. In the 400 m^2 gap and understorey, PPFD was not significantly different between seasons.

(5) The percentage of available PPFD reaching the understorey was highest on cloudy, overcast days and lowest on sunny days. No correlation was found between daily total PPFD in the 400 m^2 gap centre and in the adjacent understorey measured on the same days.

(6) In the clearing, a high proportion of 10-min averages were greater than 500 μmol m^{-2} s^{-1}; in the 400 m^2 gap, a high proportion of 10-min averages were between 100 μmol m^{-2} s^{-1} and 500 μmol m^{-2} s^{-1}; in the understorey over 70% of the 10-min averages were below 10 μmol m^{-2} s^{-1}. The clearing exhibited the greatest diurnal variation in PPFD and the least day-to-day variation, whereas the understorey exhibited the least diurnal variation and the greatest day-to-day variation in PPFD.

INTRODUCTION

Photosynthetic photon flux density (PPFD), in the waveband 400–700 nm, plays a major role in the growth, survival, and regeneration of tropical rain forest plants (Richards 1952; Schulz 1960; Longman & Jeník 1974; Whitmore 1975). Beyond this fundamental observation, however, very little is known about how light regimes vary in different forest microhabitats. This study was undertaken to compare diurnal and seasonal patterns of PPFD in a range of rain forest habitats within a single lowland forest in Costa Rica. While data on photosynthesis and growth are lacking for most rain forest species (Mooney *et al.* 1980), detailed descriptions of characteristic forest light environments will provide a much needed framework for future studies on the ecophysiology and dynamics of rain forest vegetation. Several important descriptions of the distribution of light in tropical rain forests throughout the world have been published (Evans 1939; Ashton 1958; Whitmore & Wong 1959; Odum, Drewry & Kline 1970; Brinkman 1971; Björkman & Ludlow 1972; Yoda

1974). Virtually no data are available which allow comparisons between characteristic environments within the same forest type (Schulz 1960; Bazzaz & Pickett 1980).

Mature tropical rain forests are dynamic communities with a high frequency of natural disturbance (Webb, Tracey & Williams 1972; Connell 1978; Hartshorn 1978; Whitmore 1978). The patchy and discontinuous nature of the canopy results in highly variable patterns of light availability in understorey and gap environments. Large disturbances, such as multiple tree falls, completely alter the microclimate. The forest may be considered a mosaic of patches in different stages of growth, with each stage receiving different amounts of light and other resources (Watt 1947; Richards 1952; Bazzaz & Pickett 1980; Denslow 1980). In order to evaluate the responses of species to a range of light conditions, it is necessary to know the nature of the light environments experienced by these species.

Toward this end, we set out to describe patterns of PPFD in four forest sites: a large clearing, a large gap, an average-size gap, and heavily shaded understorey. The two questions guiding the study were: (i) How does PPFD vary within and between these forest habitats, and (ii) Is there seasonal variability in light availability?

STUDY AREA

The study was conducted at Finca La Selva (10°26′N), at an altitude of 37–100 m in the Atlantic lowlands of Costa Rica. The vegetation is classified as tropical premontane wet forest (Holdridge *et al.* 1971). The mean annual rainfall is about 4000 mm with appreciable amounts every month (Frankie, Baker & Opler 1974). There is usually a drier season from January–April and often a short dry period in September–October, but there is high year-to-year variability. The mean monthly temperature is 24 °C (Frankie, Baker & Opler 1974).

Most of La Selva is covered by tall, mature forest with some trees over 50 m in height. The canopy is discontinuous, with frequent gaps due to tree falls. Nearly half of the tree species are dependent on gaps for successful regeneration (Hartshorn 1980). A turnover rate of 118 years has been estimated from data on gap size and frequency (Hartshorn 1978). More detailed information on the climate, phenology, and composition of the vegetation can be found in Holdridge *et al.* (1971), Hartshorn (1972), and Frankie, Baker & Opler (1974).

MATERIALS AND METHODS

Equipment and sampling

Measurements of PPFD were made using quantum sensors constructed according to Biggs *et al.* (1971), which were connected to a battery-powered data-logger (Campbell Scientific CR-21). The data-logger monitored up to six sensors at 10-s intervals and computed 10-minute averages of PPFD. Ten-minute averages were used because this time interval is sufficiently short to indicate sunfleck events while keeping the quantity of data which must be analysed to manageable levels. Sensors were calibrated with a standard quantum sensor (Li-Cor Inc., LI-190SB) under uniform full sun conditions. Frequent calibrations were done to ensure that all sensor readings remained within 5% of the standard.

During sampling periods, PPFD was monitored continuously for 3–10 days at each site during the wet and dry seasons. Data were not collected during *temporales*, which are extremely rainy periods when the sky may be overcast for several days at a time. Neither were data collected during one of the infrequent dry periods that are known to last for 2–3 weeks. Sampling days at each site include at least one sunny day and one overcast or rainy day, and presumably represent all but the extreme conditions mentioned above.

Sites

Four sites were selected for detailed PPFD measurements: heavily shaded understorey, two gaps, and a 0·5 ha clearing. These sites were chosen to span the range of light environments present at La Selva. The 200 m^2 gap measured 17 m east–west and approximately 10 m north–south, and the 400 m^2 gap measured 40 m north–south and 12 m east–west. Both gaps were less than 1 year old and were approximately rectangular. Sensors were placed in the centre of the gaps.

The shaded understorey site was approximately 10 m east of the 400 m^2 gap; this permitted the simultaneous measurement of gap and understorey PPFD. During the wet season, clearing PPFD measurements were made in a recently cut, 0·5 ha plot. Because of the rapid growth of the vegetation in this plot, a 1·0 ha clearing adjacent to a palm plantation was used for the dry season PPFD measurements.

Measurements were made during the 1981 wet season and the 1982 dry season. In the clearing, 400 m^2 gap, and understorey sites measurements were made for 6 days in the dry season and 7 days in the wet season. In the 200 m^2 gap site measurements were made for 8 consecutive days during the dry season only. Sensors were placed at a height of 0·7 m in the gap and understorey sites, and at 2·0 m in the clearings. Two quantum sensors were used at each site. The sensors were supported in a horizontal position within 3 m of each other. Due to the limited number of sensors and the small size of each sensor, it was not possible to account completely for spatial variation within each site.

Data analysis

Daily averages were calculated for each sensor from the 10-min average data. These values were then averaged for the two sensors at each site. The day length at La Selva is approximately 12 h; it varies by 50 min throughout the year. Daily averages were multiplied by total day length to obtain daily total PPFD.

The days of minimum, median, and maximum total PPFD were determined for each site during the wet and dry seasons. Frequency distributions of 10-min averages were calculated for each of these days, using intervals that were considered relevant for measurable photosynthetic parameters. Smoothed daily curves were drawn following Tukey (1977). Box and whisker diagrams (Tukey 1977) were used to compare the range and location of daily average PPFD between sites and between seasons. Student's *t*-test for unequal variances was used to compare daily total PPFD for wet and dry seasons at each site.

RESULTS

Photosynthetic photon flux densities in the four sites are summarized in Table 1 and Fig. 1. Measurements between the sites differed by more than two orders of magnitude. Daily average PPFD ranges from less than 5 $\mu mol\ m^{-2}\ s^{-1}$ in the deeply shaded understorey to over 600 $\mu mol\ m^{-2}\ s^{-1}$ in the clearing. The highest daily total PPFD, obtained in the clearing during the dry season, was 33·9 mol m^{-2}. Daily total PPFD in the understorey never reached 1·0 mol m^{-2} and rarely exceeded 0·5 mol m^{-2}. Daily total PPFD in the understorey, 200 m^2 gap, and 400 m^2 gap were 1–2%, 9%, and 20–35%, respectively, of PPFD in the clearing during both seasons. During the dry season, daily total PPFD in the

TABLE 1. Values of daily average (μmol m^{-2} s^{-1}) and total daily (mol m^{-2}) photosynthetic photon flux density on minimum, median, and maximum days in four tropical rain forest sites in Costa Rica during wet and dry seasons. Values are averages of two adjacent quantum sensors.

	Clearing		400 m^2 gap		200 m^2 gap	Understorey	
	Wet	Dry	Wet	Dry	Dry	Wet	Dry
Minimum							
Average	316	493	89·4	95·6	35·2	5·32	4·12
Total daily	13·7	21·3	3·86	4·13	1·52	0·23	0·18
Median							
Average	530	643	150	145	59·3	7·87	5·92
Total daily	22·9	27·8	6·50	6·27	2·56	0·34	0·26
Maximum							
Average	724	778	314	165	71·1	12·7	11·6
Total daily	33·9	33·6	13·6	7·14	3·07	0·55	0·50

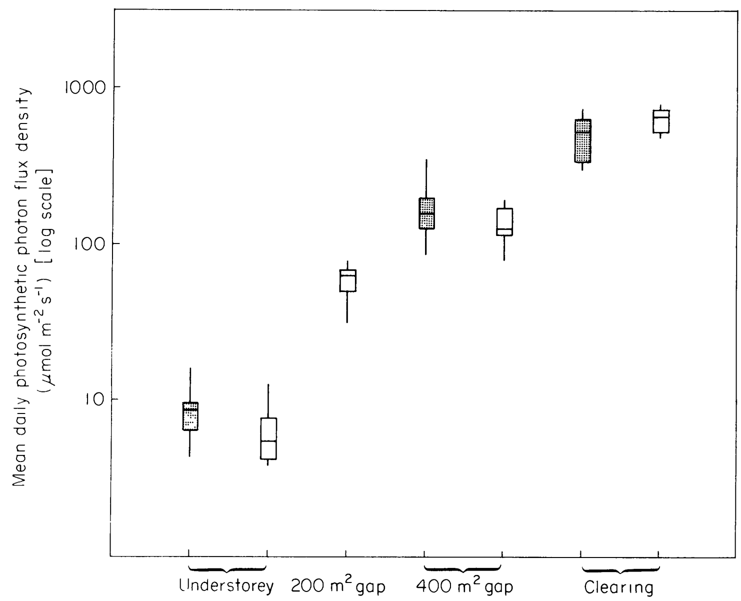

FIG. 1. Schematic log plot of daily average photosynthetic photon flux density (μmol m^{-2} s^{-1}) in four sites in tropical rain forest in Costa Rica during (▦), wet and (□), dry seasons. The centre bar denotes the median day measured; upper and lower bars represent the 75th and 25th percentile, respectively; vertical lines connect the minimum and maximum days measured.

400 m^2 gap was, on average, 2·4 times greater than in the 200 m^2 gap, and 20–25 times greater than in the understorey. In the 200 m^2 gap, daily total PPFD was 9 times greater than in the understorey.

In the clearing, a significant difference was found between the mean daily total PPFD measured during the wet and dry seasons (t = 2·23, d.f. = 20, P = 0·037), with a 24% higher daily total PPFD during the dry season. In contrast, the daily total PPFD in the 400 m^2 gap and understorey sites did not differ significantly between seasons (400 m^2 gap: t = 1·38, d.f. = 19, P = 0·183; understorey: t = 1·82, d.f. = 23, P = 0·082).

The diurnal pattern of PPFD on the clearest day measured in each habitat is illustrated in Fig. 2. In the clearing, PPFD exceeded 1000 μmol m^{-2} s^{-1} for approximately 5 h; the

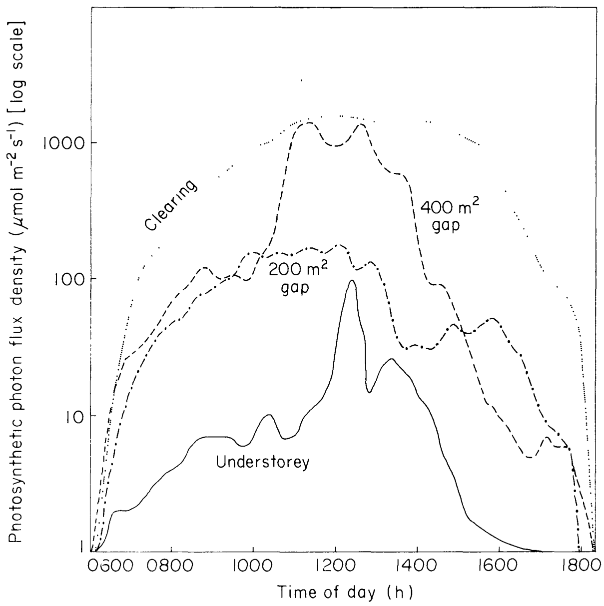

FIG. 2. Log plot of the daily pattern of photosynthetic photon flux density (μmol m^{-2} s^{-1}) in tropical rain forest in Costa Rica for one clear, sunny day in a 0·5 ha clearing, a 400 m^2 gap, a 200 m^2 gap, and an understorey site.

maximum 10-min average reading was 1828 μmol m^{-2} s^{-1}. In the large gap, the period of direct radiation was reduced to only 2 h, and the peak 10-min average reading was 1559 μmol m^{-2} s^{-1}. Relatively little direct radiation reached the 200 m^2 gap, and the PPFD rarely exceeded 200 μmol m^{-2} s^{-1} during the dry season. In the understorey PPFD was extremely low; 10-min averages were generally less than 10 μmol m^{-2} s^{-1}, except during sunflecks, when PPFD exceeded 100 μmol m^{-2} s^{-1} for brief periods. Ten-minute averages of PPFD obscured much of this short-term variation.

The extreme differences in the light environments of these habitats are further illustrated by means of frequency distributions of 10-min average PPFD readings on days with minimum, median, and maximum daily total PPFD (Figs 3–5). On the days with maximum PPFD in the clearing, over 40% of the 10-min readings were over 1000 μmol m^{-2} s^{-1} (Fig. 5). Relatively few 10-min readings were below 100 μmol m^{-2} s^{-1} in the clearings; during the median days of both seasons, less than 20% of the 10-min averages were below 100 μmol m^{-2} s^{-1} (Fig. 4).

In the 400 m^2 gap, relatively few 10-min averages were above 1000 μmol m^{-2} s^{-1}; on the day with maximum PPFD in the wet season, 11% of the readings were above 1000 μmol m^{-2} s^{-1} (Fig. 5). In the large gap, PPFD was concentrated between 100 μmol m^{-2} s^{-1} and 500 μmol m^{-2} s^{-1} on minimum and median days (Figs 3 & 4), with a relatively high proportion of 10-min averages below μmol m^{-2} s^{-1} (Figs 3–5). In the smaller 200 m^2 gap, most of the 10-min averages were below 100 μmol m^{-2} s^{-1}; only 32% of the readings exceeded 100 μmol m^{-2} s^{-1} on the day with maximum PPFD (Fig. 5).

In the understorey, 74–100% of the 10-min averages were below 10 μmol m^{-2} s^{-1} (Figs 3–5). During the wet season, there was an increased proportion of PPFD readings in the 10–25 μmol m^{-2} s^{-1} range, indicating higher diffuse radiation (Figs 3 & 4). Ten-minute

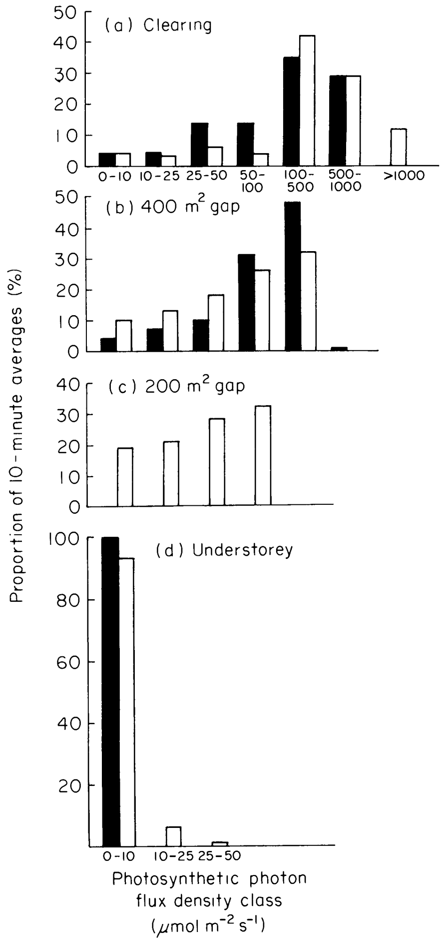

FIG. 3. The proportion of 10-min average photosynthetic photon flux density readings in different intensity classes on the minimum day measured in tropical rain forest in Costa Rica during (■), wet and (□), dry seasons in: (a), 0·5 ha clearing; (b), 400 m^2 gap; (c), 200 m^2 gap; and (d), understorey sites.

average readings above 25 μmol m^{-2} s^{-1} were generally due to sunflecks, which were often less than 5 min duration. Readings of PPFD during sunflecks were generally between 100 μmol m^{-2} s^{-1} and 500 μmol m^{-2} s^{-1}. Despite their low frequency (3–4%) over the course of the day, sunflecks contributed 55% and 77% of the daily total PPFD on the maximum days in the wet and dry seasons, respectively.

The simultaneous measurements of PPFD in the 400 m^2 gap centre and adjacent understorey are summarized in Table 2. The proportion of understorey to gap PPFD is not significantly different between seasons (Mann–Whitney *U*-Test, $P = 0{\cdot}80$). Weather conditions were recorded during the wet season and indicate that a higher proportion of understorey to gap PPFD occurred on cloudy, overcast days, which were more common during the wet season. On 2 July and 31 August, the sunniest days sampled, the proportion of PPFD in the gap that reached the understorey was reduced (Table 2). It is clear from these results that light in the understorey was not a simple function of the incident PPFD.

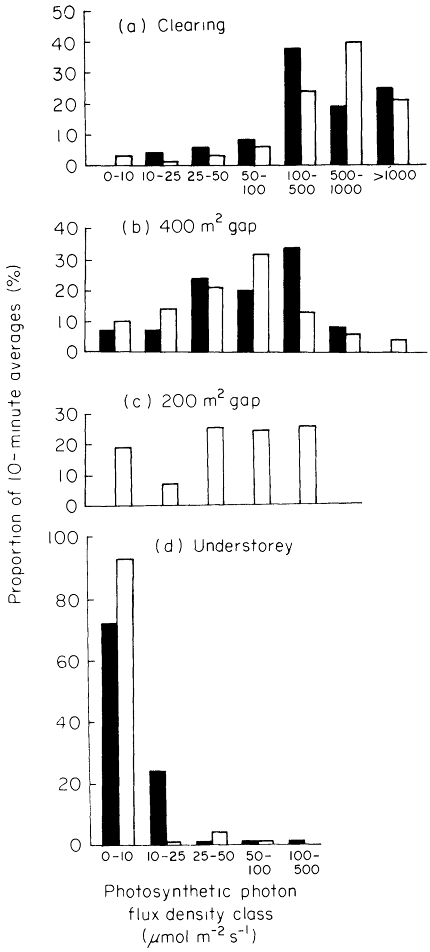

FIG. 4. The proportion of 10-min average photosynthetic photon flux density readings in different intensity classes on the median day measured in tropical rain forest in Costa Rica during (■), wet and (□), dry seasons in: (a), 0·5 ha clearing; (b), 400 m^2 gap; (c) 200 m^2 gap; and (d), understorey sites.

No significant correlation was found between the total daily PPFD measured in the gap centre and in the adjacent understorey on the same days (Spearman Rank Test, $rs = 0{\cdot}320$).

The range and distribution of daily average PPFD in the four sites are presented in Fig. 1. Considerable day-to-day variation was found in each site. The coefficient of variation ranged from 14·9 for the clearing in the dry season to 44·4 in the understorey in the dry season. In the clearing and the 400 m^2 gap, the coefficient of variation was higher during the wet season. During both seasons, the understorey had a higher coefficient of variation than the clearing. Within the range of weather conditions on sampling days, the variation from day to day in all the sites was considerably greater than seasonal variation (Fig. 1).

Although the spatial variation in PPFD was not rigorously measured in this study, considerably more variability was found between the two adjacent quantum sensors in the understorey site than in the other three sites. It was not unusual to find that average PPFD

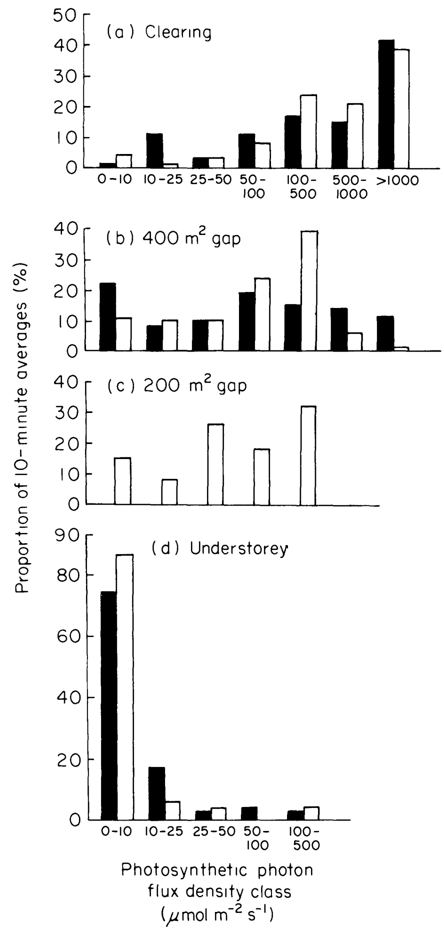

FIG. 5. The proportion of 10-min average photosynthetic photon flux density readings in different intensity classes on the maximum day measured in tropical rain forest in Costa Rica during (■), wet and (□), dry seasons in: (a), 0·5 ha clearing; (b), 400 m^2 gap; (c), 200 m^2 gap; and (d), understorey sites.

readings from sensors less than 3 m apart would differ by a factor of two or greater. These differences were most pronounced for instantaneous readings and appear to reflect a high degree of spatial variation in sunflecks rather than in diffuse PPFD.

DISCUSSION

The high degree of variability in the light environment within and between the four sites can be interpreted on several time scales. On a diurnal basis, the clearing shows the most extreme fluctuations and the broadest range in PPFD (Fig. 2). On a day-to-day basis, however, the clearing exhibited the lowest coefficient of variation for daily quantum flux measurements. In contrast, the heavily shaded understorey site was the least variable on a diurnal basis and the most variable on a day-to-day basis. The two gaps were intermediate in variability at both time scales.

TABLE 2. Comparisons of photosynthetic photon flux density in a 400 m^2 gap and adjacent heavily shaded understorey in a tropical rain forest in Costa Rica. Measurements are 12-h daily totals (mol m^{-2}), averaged for two adjacent quantum sensors. Understorey PPFD as a percentage of gap PPFD is calculated for each day.

Date	Understorey	Gap	Understorey/gap (%)
Wet season 1981			
1 July	0·31	5·25	5·8
2 July	0·55	13·6	4·1
3 July	0·42	6·40	6·6
27 August	0·31	6·86	4·5
28 August	0·23	3·86	6·0
30 August	0·40	6·60	6·2
31 August	0·34	8·51	4·0
Dry season 1982			
27 January	0·18	6·36	2·8
28 January	0·25	6·27	4·0
29 January	0·22	4·13	5·2
30 January	0·26	6·95	3·8
31 January	0·22	7·13	3·2
1 February	0·50	5·03	9·9

Seasonal variability in PPFD was evident in the clearings. The lower frequency of cloud cover during the dry season resulted in increased direct solar radiation, despite the lower solar angles during these months (Fig. 6). During the wet season, increased solar elevation resulted in more direct radiation at solar noon on clear days (Fig. 6), based on calculations using equations in Lee (1978). This effect is seen in the highest single daily total PPFD measurement on 11 September. However, the wet season was characterized by more cloud which reduced the available radiation levels substantially.

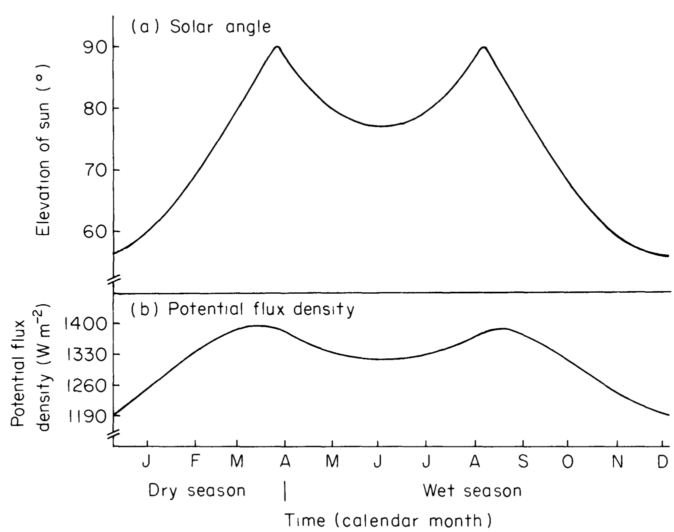

FIG. 6. Annual changes in (a), solar angle; and (b), potential flux density, at solar noon at 10°26′N. Solar constant of 1400 W m^{-2} is assumed. The monthly values are plotted for the 22nd day of each month. Potential flux densities were calculated using equations discussed in Lee (1978).

The lack of seasonal differences in light availability in the understorey and gap sites may also be due to the interaction of cloud conditions and solar elevation. At high solar angles, optical path lengths through the forest decrease, allowing greater penetration of beam radiation. Beam enrichment of diffuse radiation within the forest also increases with solar elevation and leafiness of the canopy (Hutchison & Matt 1976). Both of these factors should lead to an increase in diffuse radiation during the wet season, when solar elevation and canopy density are highest (Frankie, Baker & Opler 1974). The results presented in Figs 3–5 support the view that higher intensities of diffuse radiation occur during the generally overcast days of the wet season.

Few generalizations can be made about seasonal variation in PPFD within and between sites. This is, in part, due to the high year-to-year variability in the degree of seasonality. Also, the small number of days sampled during each season may not be representative. The finding that day-to-day variability within sampling periods at any one site is greater than seasonal variability underscores the primary importance of daily cloud cover compared to annual changes in solar elevation.

To interpret patterns of variability in PPFD within and between the sites, it is important to consider the photosynthetic light responses of the plants which grow there. In heavily shaded understorey environments, where photosynthesis is occurring at less than 10 μmol m^{-2} s^{-1}, the response of photosynthesis to relatively small changes in PPFD is likely to be linear or nearly so (R. L. Chazdon, unpublished). Variations in PPFD of a small magnitude may have a large effect on carbon gain in the understorey as compared to a large clearing, where photosynthesis may be at or near saturation for much of the day.

Few data are available for detailed comparisons of the light environments at La Selva with those of other tropical rain forests. Björkman & Ludlow (1972) measured PPFD in a subtropical rain forest in Queensland, Australia, using quantum sensors similar to those used in the present study and obtained daily total PPFD values of 0·21 mol m^{-2} at the forest floor. Average values of daily total PPFD in an open site were 44·2 mol m^{-2}, which is higher than the maximum value recorded in the clearing at La Selva. An average of 0·48% of PPFD incident on the canopy reached the forest floor, indicating considerably lower transmission values as compared to La Selva.

In an evergreen subtropical forest understorey on Oahu, Hawaii, transmission values ranged from 1·5–3·8% full sun (Pearcy 1983). Daily total PPFD ranged from 0·55 mol m^{-2} to 1·38 mol m^{-2} in nine sites measured from June–August 1980. Approximately 40% of the total PPFD in the understorey during this period was contributed by sunflecks; on clear days this percentage reached 80%. The mean daily total PPFD measured in the open during the sampling period was 35·4 mol m^{-2}; this is also higher than the maximum PPFD measured in the clearing at La Selva.

As compared to open areas at less equatorial latitudes, the clearings at La Selva have lower total daily PPFD (Table 1). This pattern may have been the result of the shorter day length as well as the interaction between cloudiness and humidity (Lee 1978; Bazzaz & Pickett 1980). The differences in the proportion transmitted between La Selva and the other forests are less easily explained, but may result from differences in the architecture of forest canopies.

There are very few published data on the light environments of gaps in temperate or tropical forests (Schulz 1960; March & Skeen 1976). Various measurements of gap size distributions at La Selva have been made (Hartshorn 1978; Sanford, Braker & Hartshorn 1982); mean gap size is 162 m^2 (G. S. Hartshorn, personal communication) and gaps between 40 m^2 and 200 m^2 are the most frequent size classes (Sanford *et al.* 1982).

Therefore, the measurements of PPFD in the gaps described in this study are presumably higher than PPFD for most gaps at La Selva. However, the gap light environments described here may be representative of much of the total gap area.

At present, a deeper understanding of the ecology and dynamics of rain forest vegetation is constrained by the lack of data on the physiological responses to environmental variability. Studies on photosynthetic responses to rapid fluctuation in light intensity, phenotypic plasticity in photosynthetic light responses, and ontogenetic changes in photosynthetic capacity in tropical rain forest species are of particular importance. Laboratory and field research on photosynthetic responses and growth rates of understorey, gap, and pioneer species in a range of habitats will provide a basis for the integration of ecophysiological processes and regeneration patterns. Such an integration is essential for the development of rain forest management programmes.

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