Abstract

Photosynthetic photon flux density (PPFD; μmol photons m⁻² s⁻¹) regimes within vegetation canopies are intrinsically heterogeneous in time and space. Photosynthesis responds to changes in the intensity and temporal variability of PPFD in a non-linear way. Therefore, it is important to quantify PPFD heterogeneity at short time scales in order to better understand and assess plant–atmosphere carbon exchange from the scale of the individual leaf to the entire canopy. Here, we report the intensity and temporal heterogeneity of sunflecks at three heights within a 42 m tall, monodominant *Gilbertiodendron dewevrei* tropical rain forest canopy in central Africa over a 12-day measurement period. Overall, sunflecks occurred during an average of 0.7% of the total sample time and contained 9.5% of the total recorded energy. These values ranged in magnitude with canopy height, as did the average intensity of PPFD contained in sunflecks. Probability distributions of sunfleck intensities were positively skewed at all three measurement heights. The temporal separation of sunflecks was bimodal at all three measurement heights; for example, at 3 m above ground level (AGL), 85% of all sunflecks were separated by either less than 30 s (43%) or more than 32 min (42%). Sunflecks were clustered in time such that 68, 84, and 89% of all sunflecks at respective heights of 3, 24, and 34 m AGL fell within clusters where no more than 2 min of non-sunfleck PPFD separated temporally adjacent sunflecks. This, plus the fact that a large percentage of the time within the clusters is comprised of sunfleck-level PPFD, indicates that sunfleck clusters are of great importance for photosynthesis within the canopy. We discuss the data from this site in the context of recent measurements and models of dynamic photosynthesis and present some possible implications for photosynthetic processes within a dense tropical forest canopy. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: *Gilbertiodendron dewevrei*; Light; Monodominant forest; PAR; Photosynthetically active radiation; PPFD; Spatial autocorrelation; Sunflecks; Sunfleck clusters; Tropical rain forest canopy

1. Introduction

Photosynthetic photon flux density (PPFD; μmol photons m⁻² s⁻¹) regimes within vegetation canopies are intrinsically heterogeneous in time and space. Many plant ecophysiological processes respond non-linearly to changes in the intensity and temporal variability of PPFD. Therefore, accurately characterizing PPFD heterogeneity is important to predict rates of photosynthesis within a canopy (e.g. Norman, 1982, 1993; Baldocchi and Harley, 1995; de Pury and Farquhar, 1997; Pearcy et al., 1997; Kirschbaum et al., 1998). In addition, because some species are genotypically suited for specific light regimes, understanding heterogeneity of...
the PPFD regime within canopies may be important for assessing vegetation regeneration, growth, and succession (e.g. Pearcy, 1983; Oberbauer et al., 1993; Canham et al., 1994; Watling et al., 1997).

Over the past decade, much effort has been made to quantify the time-course of foliar carbon gain and to describe the biochemical dynamics of foliar photosynthesis during rapidly fluctuating PPFD conditions (e.g. Pearcy et al., 1985; Chazdon and Pearcy, 1986a, b; Kirschbaum and Pearcy, 1988a, b; Tinoco-Ojanguren and Pearcy, 1992; Kursar and Coley, 1993; Sassenrath-Cole et al., 1994; Valladares et al., 1997; Zipperlen and Press, 1997). These investigations have led to the development of physiologically-based models of dynamic photosynthesis that are applicable to assessing foliar carbon gain within plant canopies (Gross et al., 1991; Pearcy et al., 1997; Kirschbaum et al., 1998). Coupling such dynamic photosynthesis models with empirical field measurements of PPFD heterogeneity within a canopy is necessary to evaluate the contribution of middle- and under-story leaves to whole-canopy carbon gain. Because foliar photosynthetic induction state and radiation use efficiency (RUE; moles of carbon assimilated per mole of incident photons) vary according to the frequency and duration of sunflecks (short-lived, bright patches of PPFD; e.g. Pearcy et al., 1985; Chazdon and Pearcy, 1986a, b; Sharkey et al., 1986; Kirschbaum and Pearcy, 1988a, b; Sassenrath-Cole and Pearcy, 1994), these field measurements must be temporally explicit with time scales on the order of seconds to minutes.

Many studies have investigated various aspects of PPFD heterogeneity within natural and agricultural canopies (see reviews by Chazdon, 1988; Pearcy, 1990; Baldocchi and Collineau, 1994), but few studies quantify the temporal variability of sunflecks at a fine enough scale to use in concert with dynamic models of foliar photosynthesis. In one such comprehensive study, Pearcy et al. (1990) reported frequency distributions of the duration of sunflecks, the time between sunflecks, and sunfleck intensity at various heights within a soybean canopy. For studies within tropical rain forests, high time resolution PPFD data have been limited to measurements near ground level (Pearcy, 1983; Valladares et al., 1997). In order to better assess the time course of carbon exchange for leaves occurring within forest canopies, additional measurements of temporal sunfleck variability are required not only near the ground, but also at height within the canopy. Such measurements may provide insight into the actual contribution of within-canopy leaves to whole-canopy carbon exchange with the atmosphere over longer (hourly to daily) time scales.

The main objective of this study is to characterize the intensity and temporal heterogeneity of sunflecks at three heights within a central African tropical rain forest canopy. The measurements were made within a naturally-occurring, monodominant forest canopy comprised almost wholly of the leguminous, evergreen species *Gilbertiodendron dewevrei* (De Wild.) Leonard (Caesalpiniaceae). We report the PPFD measurements in the context of leaf photosynthesis and leaf area index (LAI; leaf area per unit ground area) at these three heights in order to relate the PPFD regimes to leaf ecophysiology and canopy structure. The PPFD records are analyzed in a similar fashion to those reported by Pearcy et al. (1990) in order to characterize components of light heterogeneity known to be important to temporal photosynthetic dynamics, including sunfleck intensity, sunfleck duration (e.g. Chazdon and Pearcy, 1986b), and the duration of the low-light intervals between sunflecks (Sassenrath-Cole and Pearcy, 1994; Valladares et al., 1997). For example, periods where sunflecks are closely clustered together in time are compared to unclustered sunflecks to investigate how the canopy PPFD regime may affect dynamic properties of photosynthesis such as induction state (e.g. Chazdon and Pearcy, 1986a, b) and amounts of post-sunfleck CO2 fixation (e.g. Sharkey et al., 1986). A subset of the results are further analyzed with respect to changes in the above-canopy sky diffuse fraction (SDF; diffuse PPFD/total PPFD) to investigate how varying cloud and haze cover affects PPFD heterogeneity within this forest.

2. Materials and methods

2.1. Site characteristics

This study was conducted within the framework of the Experiment for Regional Sources and Sinks of Oxidants (EXPRESSO), an interdisciplinary experiment involving African, French, and US scientists (Delmas et al., 1999). All measurements were made...
between 30 November and 11 December 1996 on the periphery of Nouabálé-Ndoki National Park (hereafter referred to as ‘Ndoki’), in the northern portion of the Republic of Congo, central Africa (2°12’N, 16°24’E, elevation ~350 m). A detailed climatology of the Ndoki region is given by Fontan et al. (1992). Forests of the Ndoki region are representative of the African rain forest biome in that they contain mixed-species stands (~150–175 species per ha) occurring adjacent to monodominant stands formed by members of the Caesalpiniaceae (e.g. Gérard, 1960; White, 1983; Moutsamboté et al., 1994). In these monodominant forests, one species commonly makes up >80% of the stem basal area (Gérard, 1960; Hart et al., 1989; Hart, 1990); G. dewevrei comprises 85% of the stem basal area at the Ndoki field site (Vierling, 1999). The causes of the co-occurrence of these extensive monodominant stands alongside mixed forests are as yet unclear; they likely persist due to unique and complex combinations of ecological factors including intense competition for light (see Hart et al., 1989; Torti, 1998).

2.2. Instrumentation and sample scheme

2.2.1. PPFD measurements

We measured PPFD simultaneously at three different vertical levels within the canopy to assess sunfleck dynamics with increasing canopy depth. Single rope techniques were used (e.g. Perry and Williams, 1981) to place sensors high within the canopy and to minimize human disturbance of the canopy light regime. PPFD measures at each level were attained using custom-built ceptometers, each consisting of a 1.8 m linear array of gallium arsenide phosphide photodiodes (GaAsP; Model G 1118, Hamamatsu Corporation, Hamamatsu City, Japan; Gutschick et al., 1985; Pearcy, 1989) spaced 6 cm apart. Prior to placement in the canopy, each photodiode was calibrated under sunlight against a quantum sensor (Model 190SA, Li-Cor Corporation, Lincoln, NE). Each sensor was leveled and individually wired to an analog relay multiplexer (Model AM416, Campbell Scientific, Inc., Logan, UT) strapped to a tree branch, which was in turn wired to a multiple-channel data logger (Model CR10X, Campbell Scientific, Inc.) on the ground. The top of the canopy reached an approximately uniform height of 42 m. The top and middle ceptometers each contained 30 GaAsP photodiodes and were placed at 34 and 24 m AGL, while the bottom ceptometer contained 29 sensors placed at the height of 3 m AGL. Each ceptometer was supported by an aluminum boom and placed such that there were no large branches in line with the solar path within 5 m of the ceptometer. The location and orientation of each ceptometer were changed once every ~3 days over the 12-day period to increase spatial coverage at the three canopy heights. In addition, we gathered PPFD measurements at 1 m AGL using a quantum sensor mounted atop a motorized tram traveling back and forth along a 20 m long cable at a rate of 1 cm s⁻¹.

Readings from each of the 89 ceptometer sensors were recorded once every 1.5 s (0.67 Hz). This sample rate was chosen for two principal reasons. First, 1.5 s provided sufficient time for the data acquisition system to reliably sample all sensors and avoid aliasing. Second, results from previous empirical studies yielded insights on the appropriate sampling rate to use. In a soybean canopy sunflecks with a duration ≤1.6 s accounted for only 6.7% of the sunfleck PPFD (Pearcy et al., 1990), while the mean sunfleck length near the floor of an Australian tropical rain forest canopy was 50 s (Pearcy, 1988). Therefore, we surmised that in this forest canopy the value of the information gained using a larger number of sensors and a 1.5 s sample rate was likely to outweigh the alternative of fewer sensors and more rapid sampling. Measurements were acquired and continuously downloaded to a laptop computer between sunrise and sunset; during the 12-day sample period, 93% of the daytime periods were successfully sampled.

During the sample period, sky conditions varied from clear to heavily overcast. Measurements of total and diffuse PPFD were acquired from the top of a 60 m tall tower situated approximately 700 m west of the canopy site using two quantum sensors mounted upon a stationary shadow band platform oriented so that one sensor was shaded throughout the day (after Horowitz, 1969). These above-canopy measurements provided a reference point for the within-canopy observations.

2.2.2. Ancillary measurements

In order to place the PPFD data into context with canopy structure and leaf ecophysiology, we also gathered measurements of LAI and leaf photosynthesis.
along the vertical profile. Upward-looking, nearly hemispherical photographs of the canopy were acquired during overcast skies to quantify both LAI and the relative annual variability of canopy openness along the solar path. Hemispherical photographs were acquired using a camera (Pentax K-1000) fitted with a combination of a 19 mm wide-angle lens (Vivitar, Inc.) and a fish-eye conversion lens (Pro-Optics, Inc.) to produce an effective focal length of 8 mm. Lens distortion was characterized in the laboratory prior to field deployment. Hemispherical photographs were taken at 1, 2, 4, 8, 12, 16, 20, 24, 28, 32, and 36 m AGL, as well as at points adjacent to each ceptometer location using panchromatic film (T-MAX, ASA100, Kodak). For each photo, care was taken to level the camera and align the image with true north.

In situ measurements of foliar photosynthesis were made on leaves occurring near the three ceptometers (at heights of 30, 20, and 1 m AGL, respectively) using a Li-Cor 6400 portable photosynthesis system. Photosynthesis measurements are described in detail in Vierling (1999). We analyzed the relation between net photosynthesis and PPFD in order to discern the approximate light saturation point (the point above which additional light caused no appreciable increase in carbon gain) at each canopy level. While previous studies have used various criteria for classifying sunflecks (see Chazdon, 1988), choosing a sunfleck threshold value near the photosynthetic light saturation point is useful for studies of foliar carbon gain at leaf and canopy scales because it helps to separate the photosynthetic activity of leaves at unsaturating PPFD from those periods when photosynthesis is PPFD-saturated (see application of this idea in the canopy modeling efforts by Sinclair et al., 1976; Norman, 1982; de Pury and Farquhar, 1997).

2.3. Data processing

We analyzed the within-canopy PPFD measurements using a modified version of the BASIC program ‘HISTO’ (R.W. Pearcy, unpublished work). Each raw PPFD data file was processed with respect to the sunfleck threshold value for the given layer. From each raw data file, the program calculates the total PPFD, the proportion of total PPFD contained within sunflecks, the peak and average intensities of PPFD during sunflecks, the duration of sunflecks, and the time elapsed since the last sunfleck for each sensor. We calculated the probability distributions of all sunfleck variables in order to assess the character of the PPFD heterogeneity within the canopy. In addition, we grouped the sunflecks into ‘clusters’ by evaluating the length of the low-light periods between the flecks and grouping those that occurred within a given time interval of one another into the same cluster (after Pearcy et al., 1990). We separately characterized clusters defined as two or more sunflecks containing arbitrarily chosen low-light interval thresholds (LLITs) between them of no more than 1.5, 3, 4.5, 6, 7.5, 9, 15, 30, 45, 60, 90 and 120 s.

We calculated the spatial autocorrelation of the within-canopy PPFD data irrespective of sunfleck thresholds. These calculations were performed with an Interactive Data Language (IDL) computer routine (R.E. Kennedy, unpublished work) using algorithms presented by Isaaks and Srivastava (1989). Autocorrelation calculations were performed for periods during which the sky diffuse fraction (SDF; diffuse PPFD above canopy/total PPFD above canopy) remained stable within the range classes of: <0.5 (mostly clear), 0.5–0.59, 0.6–0.69, 0.7–0.79, 0.8–0.89, 0.9–0.95, and >0.95 (overcast).

LAI was estimated using a multiple step digital analysis of the hemispherical photographs. Using standard image processing software (ENVI; Research Systems, Inc.), we first masked obvious tree trunk and branch portions of the photograph, and then calculated the total gap fraction (i.e. open sky pixels/total pixels) in the unmasked portions of 10° wide annular rings. These gap data were then input to a gap fraction radiative transfer inversion model (Norman and Campbell, 1989) to calculate LAI. Only the annular rings extending to a zenith angle of 60° in the photograph were utilized in order to preclude possible errors associated with transmission data from larger (near-horizon) zenith angles (after Chason et al., 1991).

Canopy openness along annual solar track trajectories were calculated using the SolarCalc program (Version 6.1; Chazdon and Field, 1987; D.D. Ackery, R.L. Chazdon, unpublished work) to determine the representativeness of the sunfleck measurements made during the 12-day sample interval relative to an entire year. Estimates of sunfleck activity made using overlays of solar trajectories on hemispherical photographs have been shown to agree relatively closely
with actual measurements of sunfleck activity using photodiodes (Chazdon and Field, 1987).

3. Results

3.1. PAR transmission, vertical LAI profile, and foliar photosynthesis

Photosynthetically active radiation (PAR) is highly depleted by the dense, continuous overstory foliage characteristic of monodominant *G. dewevrei* canopies (Louis, 1947). On a mostly clear day (Julian Day 345, 10 December 1996), the PPFD incident upon the three ceptometers registered 5.1, 5.1, and 2.0% of above-canopy PPFD at 34, 24, and 3 m AGL, respectively (Table 1). The low transmission of PAR even at the level of the top ceptometer directly relates to the fact that more than half of the *G. dewevrei* canopy LAI is contained in the upper 20% of the canopy height (Fig. 1). Thus, LAI ≈ 4 even at the topmost ceptometer placement of 34 m AGL. The mean total LAI at the site, derived from five hemispherical photographs acquired at 1 m AGL, was 7.2. Over the entire 12-day measurement period, there was an average transmission of only 1.2% to a canopy height of 1 m AGL. As a result, light-demanding lianas are sparse within the canopy except near forest gaps.

Rates of steady state net photosynthesis decreased with increasing LAI depth, with average PPFD-saturated CO$_2$ fixation rates of approximately 4.5, 3.5, and 1.5 μmol CO$_2$ m$^{-2}$ s$^{-1}$ at heights of 30, 20, and 1.5 m, respectively (see Vierling, 1999). The point at which photosynthesis saturated with respect to PPFD also varied with canopy height. By evaluating the average photosynthetic light saturation points near the height of each ceptometer, we assigned sunfleck PPFD threshold values to be 200 μmol photons m$^{-2}$ s$^{-1}$ at the top and middle levels and 100 μmol photons m$^{-2}$ s$^{-1}$ in at the bottom level.

### Table 1

<table>
<thead>
<tr>
<th>Canopy height (m AGL)</th>
<th>Energy received (mol photons m$^{-2}$ per day)</th>
<th>Transmission %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Above canopy</td>
<td>31.7</td>
<td>100</td>
</tr>
<tr>
<td>34</td>
<td>1.62 (0.16)</td>
<td>5.1</td>
</tr>
<tr>
<td>24</td>
<td>1.63 (0.29)</td>
<td>5.1</td>
</tr>
<tr>
<td>3</td>
<td>0.63 (0.06)</td>
<td>2.0</td>
</tr>
</tbody>
</table>

*Measurements were successfully recorded during 98.6% of the time between sunrise and sunset on this day. Values within parentheses represent standard deviations from the mean.*

3.2. PPFD heterogeneity

PPFD was very heterogeneous within the canopy over both the course of a day (Fig. 2) and over the course of the 12-day sample period. Autocorrelation calculations reveal that the spatial PPFD heterogeneity within this canopy varied with respect to both sky diffuse fraction and canopy depth (Fig. 3). At 34 m AGL, there was a distinct difference between the spatial correlation of sensor measurements during times characterized by higher SDF (≥0.8) and those during low SDF (<0.8; Fig. 3A). While under high SDF conditions the PPFD measurements at 34 m AGL remained highly correlated across a 90 cm sensor separation distance, during clearer skies the mean correlation coefficient dropped to 0.1–0.2 for sensors spaced only 18 cm apart. In general, the mean spatial correlation coefficients did not decrease as abruptly in the lower portion of the canopy compared to higher within the canopy (Fig. 3A–C).

Analysis of the hemispherical photographs indicates that during the sample period the daily irradiance (a function of the angular position, size, and number of canopy gaps; Chazdon and Field, 1987) received...
Fig. 2. Daily tracks of PPFD above the canopy and at the three measurement heights within the canopy on 10 December 1996, a mostly sunny day. Plots at each level within the canopy show data from three arbitrarily chosen sensors positioned at 60 cm intervals along each ceptometer.

Fig. 3. Spatial auto-correlation of PPFD measurements with respect to sky diffuse fraction at (A) 34 m; (B) 24 m; and (C) 3 m AGL within the G. dewevrei canopy. Sensors were spaced 6 cm apart at each canopy height.

at each measurement height was comparable to that expected during other times of the year (Fig. 4). Of particular note is that at 24 m AGL, daily irradiance is relatively high when the sun tracks through the southern sky (including during the measurement time period), and then reaches relative minima during periods when the sun tracks across the northern sky. This is due to the impact of a tree fall gap approximately 100 m SW of the measurement location on the afternoon radiation regime at 24 m AGL.

In sum, 539, 3161 and 2910 sunflecks occurred at the respective heights of 3, 24 and 34 m AGL during the observation period. The overall length and PAR energy attributes of the sunflecks varied greatly with both canopy height and sample day (Fig. 5). Sensors recorded sunflecks during 0.7% of the total sample time, and the amount of energy contained within these sunflecks averaged 9.5% of the total recorded energy. At the height of the top ceptometer, values ranged from no sunfleck activity on three overcast days to a maximum on Julian Day 345 when sunflecks lasted 1.6% of the total time and contributed 14% of the total PPFD. At the middle ceptometer, sunfleck activity ranged from zero on the overcast days to maxima of
Fig. 4. Annual course of irradiance reaching each of the three canopy layers. Values at each layer are scaled such that the maximum value during the year equals 1. The open symbols denote the estimated daily irradiance at the midpoint of the 12-day sample period. Dashed lines represent 2nd degree polynomial fits to the data.

Fig. 5. Percent time and percent energy represented by sunflecks during the field experiment. ‘Average’ column is the average for all days at each level, with the exception of the ceptometer at 34 m, which was positioned below a tree branch at 29 m during the first 5 days of measurements (denoted by shading). The ‘Average’ column at 34 m shows the average of all days after Julian Day 339.

Fig. 6. Frequency distributions of (a) average PPFD and (b) peak PPFD reached within sunflecks at each of the three canopy heights. Numbers of sunflecks at each level denoted in figure legends. Insets show the low end (i.e. 100–200 μmol photons m⁻² s⁻¹) of the frequency distribution at 3 m in more detail.

2.4% of the time and 26% of the energy on Julian Day 345, while at the bottom ceptometer sunfleck activity ranged from zero to maxima of 0.9% of the time and 22% of the total PPFD on Julian Day 335.

The average PPFD contained in sunflecks also varied with canopy height (Fig. 6a). At 3 m AGL, 94% of all sunflecks contained an average PPFD between 100 and 200 μmol m⁻² s⁻¹. At 24 and 34 m (where PPFD values below 200 μmol m⁻² s⁻¹ were not classified as sunflecks), 45 and 52% of all sunflecks contained average PPFDs between 200 and 225 μmol m⁻² s⁻¹.

Peak PPFD values during sunflecks showed similar trends with respect to canopy height and exhibited a slight shift towards higher PPFD classes (Fig. 6b) relative to average sunfleck PPFD values. At 3 m AGL, 90% of sunflecks peaked at a PPFD between 100 and 200 μmol m⁻² s⁻¹ while at 24 and 34 m, 36 and 44%
of sunflecks, respectively, peaked between 200 and 225 μmol m$^{-2}$ s$^{-1}$.

A greater percentage of sunflecks comprised longer duration classes with increasing canopy depth (Fig. 7a). While these data suggest that a large fraction of all sunflecks are short in duration, these short sunflecks, in sum, deliver a small proportion of total sunfleck PPFD to the forest understory (Fig. 7b). For example, at 34 m AGL, sunflecks equal to or shorter than 12 s in duration accounted for only 6.4% of the total sunfleck PPFD, while those longer than 48 s accounted for 81%.

In addition to sunfleck duration, the duration of the low-light interval between sunflecks can also substantially affect foliar carbon gain via mediation of the photosynthetic induction state of a leaf (Kirschbaum and Pearcy, 1988a; Sassenrath-Cole and Pearcy, 1994; Valladares et al., 1997). Histograms depicting the time between sunflecks in the G. dewevrei canopy show that sunflecks mostly occur either quite close to one another or are spaced out over long time periods (Fig. 8). The bimodal character of these data becomes more pronounced with depth in the canopy.

At levels higher in the canopy, progressively larger proportions of all sunflecks form clusters (Fig. 9a). The percentage of sunflecks contained within clusters reaches a plateau between the low-light interval thresholds (LLITs) of 15 and 30 s (Fig. 9a). To assess how efficiently leaves might utilize light within these sunfleck clusters for photosynthesis, we calculated the amount of time within each cluster that occurred as sunfleck. For all three layers, the mean amount of cluster time as sunfleck was quite high (~97%) with an LLIT of 1.5 s (Fig. 9b). In general, at LLITs longer than 30 s, then the higher in the canopy, the less the time within each cluster is comprised of sunfleck. The mean duration of clusters defined by various LLITs is depicted in Fig. 9c.

Because photosynthesis would likely respond to clusters as if they were single sunflecks when a large percentage of the cluster time is made up of sunflecks (see Pearcy et al., 1990; Valladares et al., 1997), we also calculated histograms of cluster duration for each cluster class in order to compare their statistics to the raw sunfleck duration histogram shown in Fig. 7a. The duration of clusters defined by even a short LLIT greatly affect the frequency distributions (Fig. 10) relative to raw sunfleck duration. For example, at all

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Fig. 7. Frequency distributions of sunfleck characteristics determined from 30 sensors placed at 34 and 24 m AGL, and 29 sensors placed at 3 m AGL in a Gilbertiodendron dewevrei forest from the period 30 November–11 December 1996.

Fig. 8. Histograms depicting three time scales of the low-light period occurring prior to sunflecks at three levels within the G. dewevrei canopy.

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Fig. 9. Plots of (a) the percentage of all sunflecks falling within sunfleck clusters; (b) the percentage of cluster time that is represented by sunflecks; and (c) the mean cluster duration, each with respect to the maximum duration of the low-light interval between sunflecks used to group sunflecks into clusters. All measurements were made from 30 November–11 December 1996.

Fig. 10. Histogram of sunfleck cluster duration within the G. dewevrei canopy. A low light interval threshold (LLIT) of 4.5 s was used to define the clusters for which statistics are presented here.

three canopy heights there were more raw sunflecks of 1.5 s in duration than in any other duration class (Fig. 7a). Maximum frequencies for sunfleck clusters defined by an LLIT of only 4.5 s, however, occur at the 48–96 s class at the top and bottom ceptometer placements and at the 96–192 s class at the middle ceptometer (Fig. 10). The fact that this large shift in the frequency distribution occurs even at short LLIT durations (where, in the case of this example, with an LLIT of 4.5 s sunflecks comprise ~95% of the cluster time; see Fig. 9b) suggests that the clustered occurrence of sunflecks is likely to significantly affect carbon gain within the canopy.

4. Discussion

4.1. Forest structure, available sunlight and sunfleck intensity

Although the three ceptometers used in this study were widely distributed with respect to canopy height (i.e. ceptometers were positioned at 7, 57 and 81% of the canopy height), all three levels exhibited quite low daily PAR transmission values (Table 1). This abrupt PAR extinction is due to the dense, continuous leaf layer that forms at the top of monodominant G. dewevrei forests. In contrast, PPFD measurements along two vertical transects within a mixed Dipterocarp forest in Sumatra (Torquebiau, 1988) show PAR extinction in that forest to be much more gradual with depth. For example, 41 and 47% of the above canopy PAR in the Sumatran forest was transmitted to levels 81 and 65% of the canopy height, respectively, over the course of 6 days. While Torquebiau (1988) did not quantify the vertical LAI profile per se, inspection of PAR transmission data suggests that the Dipterocarp forest structure is quite different from that of G. dewevrei because much of the PAR extinction (i.e. the densely foliated canopy layer) occurs deeper within the canopy. Indeed, PAR transmission had dropped to 1.7% at 28% of the Dipterocarp forest canopy height (Torquebiau, 1988). Similar vertical distributions of PAR have been measured in other mixed tropical rain forests containing emergent individuals (Yoda, 1978). Therefore, the sunfleck environments reported in the present study, regardless of sample height, might all be categorized as ‘understory’ environments relative to
similar heights in other, mixed species tropical forests. The dense, continuous overstory formed by *G. dewevrei* may play a role in the ability of this species to form monodominant forests.

The similar daily integrated amount of PAR received by the upper two ceptometers (Table 1), along with results of hemispherical photo and sunfleck analyses, provides additional insight as to how the structure of the *G. dewevrei* forest affects the within-canopy PPFD regime. Although slightly more leaf area occurs above 24 m than above 34 m (Fig. 1), a tree fall gap approximately 100 m SW of the sample site allowed more PAR transmission to the 24 m level than to the 34 m level during the afternoon due to sun/gap/sensor geometry. The fact that the greatest percentages of time and energy represented by sunflecks occurred at 24 m AGL (Fig. 5) supports this idea. Frequency distributions of sunfleck intensity show that 24 m was also the level with the highest relative percentage of sunflecks averaging and peaking above 450 μmol m$^{-2}$ s$^{-1}$ (Fig. 6); many of these high-intensity sunflecks occurred during sunny afternoon periods. Torquebiau (1988) reported similar effects of canopy structure on the vertical PAR gradient. The apparent ‘inversion’ of the PAR regime between the two upper layers in that Dipterocarp forest, whereby the deeper canopy level (at 65% of the canopy height) received higher daily integrated PPFDs than the higher sensor (at 81% canopy height), was likely due to gaps at high zenith angles occurring between upper forest layer emergents.

The frequency distributions of sunfleck intensity at all three levels within the *G. dewevrei* canopy resemble those measured at other tropical rain forest understory sites in that they are positively skewed (Fig. 6; Yoda, 1978; Pearcy, 1983; Chazdon and Fetcher, 1984; Chazdon, 1986; Chazdon et al., 1988; see also Baldocchi and Collineau, 1994). This, together with the fact that sunflecks at all three levels in this tall canopy contain small proportions of the above canopy PPFD (data not shown), indicate the strong influence of penumbra on the sunfleck regime. In contrast, sunflecks in short canopies with large leaves relative to the size of the solar disk (i.e. crop canopies) possess PPFDs close to full sunlight (Pearcy et al., 1990).

The fact that the mean spatial correlation coefficients do not decrease over distance as abruptly in the lower portion of the canopy compared to higher within the canopy (Fig. 3A–C) suggests that the PPFD regime becomes more spatially homogeneous with increasing depth in this understory. This result is likely to arise from the increase of penumbral influences with depth in the canopy, because the spatial delineation between sunflecks and diffuse light becomes more ‘smeared’ with depth (Baldocchi, 1989). In addition, the trajectory of the mean spatial correlation coefficient became more decoupled from the SDF at greater canopy depth (Fig. 3). Therefore, deeper within the canopy, forest structure (i.e. canopy gap arrangement) likely plays an increasingly greater role than does sky clarity (particularly during periods characterized by intermediate SDF) in influencing PPFD heterogeneity.

4.2. Temporal aspects of sunflecks and sunfleck clusters

The frequency distribution of sunfleck duration (Fig. 7a) is in relative agreement at all three canopy heights with that reported near the ground in a 10–20 m tall Hawaiian mixed evergreen forest (Pearcy, 1983). Pearcy (1983) determined that two-thirds of all sunflecks (defined in his study as those measurements with a PPFD greater than 150 μmol photons m$^{-2}$ s$^{-1}$) lasted less than 30 s and very few lasted longer than 5 min. The duration of the low-light interval between sunflecks, however, is markedly different between these two canopies. While in the Hawaiian forest only about 5% of the sunflecks were separated by longer than 16 min (Pearcy, 1983), in the present study up to 46% of the sunflecks were separated by at least this much time (Fig. 8c). The results at Ndoki agree more closely to findings by Valladares et al. (1997), who report that an average of 26.4% of the low-light intervals between sunflecks last longer than 4 min near the floor of a rain forest canopy on Barro Colorado Island, Panama (compared to 26% lasting longer than 4 min at 34 m, 33% at 24 m, and 53% at 3 m AGL at Ndoki). The sunfleck definition threshold used by Valladares et al. (1997), however, was 50 μmol photons m$^{-2}$ s$^{-1}$. Had a higher sunfleck intensity threshold value been used by Valladares et al. (1997), the percentage of low-light intervals longer than 4 min would have been more similar to that at 3 m AGL in the *G. dewevrei* canopy. The 4 min low-light duration threshold was relevant to the study of Valladares et al. (1997) because significant losses in foliar photosynthetic induction occurred after this length of time.
With short time intervals between sunflecks, the mean time-integral of PPFD is likely to remain high, allowing understory leaves to maintain an elevated state of foliar photosynthetic induction. In their study, Valladares et al. (1997) found that more than 90% of the photosynthetic induction state remains after 120 s of low light following a sunfleck. Thus, carbon gain during clusters of sunflecks is likely to be similar to that during single sunflecks. The cluster characteristics calculated for Ndoki also support this notion because even with a cluster low-light interval threshold (LLIT) of 120 s, the longest considered in this study, the mean fraction of cluster time represented by sunflecks was 70, 79, and 82% at 34, 24, and 3 m AGL (Fig. 9b). In comparison, the mean fraction of cluster time represented by sunflecks in a soybean canopy with a cluster LLIT of only 2 s was 65% (Pearcy et al., 1990). These high sunfleck: cluster time proportions, as well as the fact that penumbra in this canopy cause more gradual changes of PPFD through time compared to the rapid full sun/full shade interplay of light in canopies with few penumbral effects (Pearcy et al., 1990), suggest that between clustered sunflecks the PPFD is likely to remain at levels nearer to sunfleck PPFD values than to the PPFD of background diffuse light. This is of consequence for foliar carbon gain because the higher the PPFD during low-light intervals between sunflecks, the greater the maintenance of photosynthetic induction state (Chazdon and Pearcy, 1986b; Sassenrath-Cole and Pearcy, 1994).

4.3. Implications for ecophysiology from leaf to canopy scales

The ability of plants to utilize sunflecks for photosynthesis depends on the intensity and temporal frequency of sunflecks due to the non-linear and hysteretic character of photosynthetic ecophysiology. Because of the great complexity of foliar carbon gain in spatially and temporally heterogeneous PPFD environments, canopy photosynthesis models typically rely upon simplified characterizations of the relationship between photosynthesis and PPFD. These simplifications fall into two categories. The first deals with the non-linearity of photosynthesis in response to light intensity. Many published canopy photosynthesis models now include radiative transfer subroutines that separate the components of direct (i.e. sunfleck; photosynthetically saturating) and diffuse (unsaturating) PPFD at arbitrary levels throughout the canopy (e.g. Norman, 1982; Baldocchi and Harley, 1995; Leuning et al., 1995; de Pury and Farquhar, 1997) and calculate the net carbon assimilation during these two light classes separately. This approach minimizes the overestimation of canopy-level photosynthesis that often occurs when average PPFDs within the canopy are applied to the non-linear response function of photosynthesis (Norman, 1993). The second model simplification deals with the response of leaves to temporal PPFD heterogeneity. While two state-of-the-art temporally dynamic models describing photosynthetic fluctuations at the leaf level have recently been published (Pearcy et al., 1997; Kirschbaum et al., 1998), much work remains to scale these dynamic models to the canopy level. A vital yet difficult step in accomplishing this scaling task lies in accurately characterizing the probability distributions of temporal sunfleck activity at various layers in the canopy. To our knowledge, no canopy photosynthesis models presently include such a routine.

While incorporating algorithms to accurately describe temporal PPFD variability and the concomitant dynamic responses of photosynthesis would add to the ‘realism’ of canopy models in how they describe photosynthesis at the leaf scale, it remains to be seen whether or not the effects of these additions would be significant at the canopy scale. For example, the amount of carbon gained by a fully induced understory leaf as a consequence of a short, bright sunfleck can be 50–300% of the carbon gain expected for the same sunfleck assuming steady-state photosynthesis (i.e. assuming a stepwise increase to the PPFD saturated rate of carbon assimilation ($A_{\text{max}}$) at the onset of a sunfleck, and then a stepwise return to background photosynthesis rates at the end of the sunfleck; Pearcy et al., 1985; Chazdon and Pearcy, 1986b; Kirschbaum and Pearcy, 1988a; Valladares et al., 1997). These high sunfleck use efficiencies (SUEs) relative to that predicted with the steady state assumption are possible for induced leaves due to the fact that high-energy photosynthetic metabolites accumulate in the leaf during sunflecks and thus enable high rates of CO₂ assimilation to briefly persist after the return to low, post-sunfleck PPFD (Sharkey et al., 1986). With increasing sunfleck length, SUE approaches values predicted assuming steady state photosynthesis (Pearcy...
et al., 1985; Chazdon and Pearcy, 1986b; Kirschbaum and Pearcy, 1988a; Valladares et al., 1997). Uninduced leaves, however, have been found to possess significantly lower SUEs than steady state predictions, even for sunflecks lasting up to 80 s (Valladares et al., 1997). Because understory leaves possess various states of photosynthetic induction and experience disparate sunfleck regimes over the course of a day, a relevant question with regard to the impact of dynamic understory carbon gain on temporally static canopy scale photosynthesis models is: do the conditions favoring high SUE (i.e. relatively high induction state and sunflecks <10 s in duration) significantly outweigh/fall short of the conditions favoring low SUE when integrated for all understory leaves over the course of a day? In other words, does the integrated daily SUE within a vegetation canopy significantly depart from the steady state assumption whereby SUE=100%?

The results from Ndoki provide some insight on this question. First, approximately half of the sunflecks occurring at all three canopy heights were separated by a low-light interval less than 30 s in length (Fig. 8c). Thus, the induction loss between these sunflecks would likely be minimal (see Sassenrath-Cole and Pearcy, 1994; Valladares et al., 1997). However, because a substantial proportion of sunflecks were also separated by low-light intervals greater than 32 min long (particularly at 3 m AGL), it is likely that many leaves in the understory possess low induction states for much of the day.

Whether these partially induced leaves are able to photosynthesize at rates significantly higher than the steady-state predicted SUE of 100% depends largely on the duration of the sunfleck. Valladares et al. (1997) found that fully-induced understory leaves exhibited SUEs near 100% during 20 s and longer sunflecks, while uninduced leaf SUEs ranged between 50–60% for a 20 s sunfleck. While we found that 54–73% of all sunflecks were shorter than 20 s in duration, a high percentage of these sunflecks were clustered closely in time. Therefore, the actual photosynthetic SUE likely depends upon the duration of these clusters. Clusters can possess high time-averaged PPFDs for much longer periods than do individual sunflecks.

Few studies have quantified the influence of heterogeneous PAR regimes on foliar photosynthesis and how estimates of predicted carbon gain assuming steady state photosynthesis differs from actual, dynamic carbon gain. In one laboratory study, Pearcy et al. (1997) found that by assuming steady state photosynthesis, actual carbon gain was overestimated by 11.5–24.4% for induced shade leaves of the Australian rain forest understory species Alocasia macrorrhiza. For uninduced leaves, the steady state model overestimated carbon gain by 38.1–50.8% (Pearcy et al., 1997). Similar experiments using leaves and canopy light regimes for soybeans failed to yield a significant difference between the actual carbon gained and that predicted using a steady state model (Pearcy et al., 1997). In a field investigation, Pfitsch and Pearcy (1989) studied the carbon gain of the redwood forest understory plant Adenocaulon bicolor and found that on sunny days the measured carbon gain was 20–30% less than that predicted using a steady state photosynthesis model under the measured sunfleck regime at the microsite. This suggests that limitations due to low photosynthetic induction state may outweigh the enhancement of carbon gained due to post-sunfleck CO2 fixation for that plant. At the canopy scale, recent comparisons of a canopy CO2 exchange model lacking a temporally dynamic component of photosynthesis with tower flux data show that the model performs quite well under a broad range of weather conditions for a temperate mixed forest (Baldocchi and Harley, 1995; Baldocchi, 1997), suggesting that the omission of a temporally dynamic description of within-canopy photosynthesis does not bias the model in that ecosystem. Additional model/tower comparisons in other vegetation types are necessary to understand the influences of temporally dynamic photosynthesis on canopy–atmosphere CO2 exchange.

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References


