Journal of Tropical Ecology (2001) 17:207–224. With 3 figures
Copyright © 2001 Cambridge University Press

Evaluation of different methods to estimate understorey light conditions in tropical forests

BETTINA M. J. ENGELBRECHT*[1] *and* HUBERT M. HERZ†

**University of Darmstadt, Institut für Botanik, Fachbereich Biologie, Schnittspahnstr. 3 - 5, 64287 Darmstadt, Germany*
†University of Bielefeld, Lehrstuhl für Experimentelle Ökologie und Ökosystembiologie, Universitätstrasse 25, 33615 Bielefeld, Germany

(Accepted 3rd August 2000)

ABSTRACT. The suitability of several methods for estimating light conditions in the understorey of tropical forests, and of different sampling schedules was evaluated. Light conditions at 16 understorey sites in a Panamanian lowland forest were continuously measured for 9 mo with quantum sensors and photodiodes. Light conditions at the sites were also assessed indirectly with hemispherical fisheye photographs, plant canopy analysis, 38-mm photographs, 24-mm photographs and a spherical densiometer. Estimates from all indirect methods, except the spherical densiometer, were highly correlated with the direct measurements. Short-term direct light measurements for a day or a week also correlated with long-term light conditions. The indirect measures differed by up to *c.* 70% from the direct measures relative to single site measurements. Hence, the indirect methods are inadequate where single site light conditions have to be assessed accurately. However, because light conditions encountered in the understorey varied up to 13-fold, the indirect methods were found to be well suited to rank understorey light conditions among a large number of sites. The results from frequent and infrequent sampling schedules differed only slightly, suggesting that taking indirect measures at the beginning and the end of a study offers a reasonable compromise between accuracy and sampling effort.

KEY WORDS: fisheye photography, hemispherical photography, light measurement, plant canopy analysis, PPFD, spherical densiometer

INTRODUCTION

Light is a crucial factor determining physiological and ecological processes in plants, as well as in animals (Denslow *et al.* 1990, Endler 1993). Among different tropical forest formations, and along climatic gradients light conditions in

---

[1] Present address: Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panamá

the understorey may vary greatly (Engelbrecht 1998). Furthermore, they are extremely variable, both spatially (horizontally and vertically) and on time scales from seconds to years (Chazdon & Fetcher 1984). Information about light in the understorey is therefore essential in many studies in tropical forests.

Assessing long-term light conditions in the understorey of forests remains a difficult task. Direct measurements are laborious and costly, and are usually only possible over a limited time span and number of sites. Several methods are frequently used to indirectly estimate light conditions. They are well established for quantifying light differences between gaps of different sizes and the understorey (Chazdon & Field 1987, Rich *et al.* 1993). However, it has not yet been shown that these indirect methods are powerful enough to actually distinguish light conditions *within* the understorey of tropical forests. In this study we explicitly focus on light conditions *within* the understorey. Average light conditions in the understorey of tropical forests are extremely low, often below 1% of the light reaching the canopy (Chazdon & Fetcher 1984, Smith *et al.* 1992). Because of the low light levels in tropical forests, measurements to assess the light environment must be precise to allow discrimination between sites within the understorey.

We empirically compared direct measurements of the photosynthetic photon flux density (PPFD) with several indirect methods of measurement, to evaluate the suitability of the latter to distinguish, and to predict the long-term light environment at microsites in the understorey of a neotropical forest.

METHODS

Study site

The study was conducted in the tropical moist forest of Barro Colorado Island, Panama (9°9′N, 79°51′W). Long-term-average annual rainfall is 2600 mm, with a pronounced dry season from December through April. Measurements were taken in 2 ha of old forest on an east-facing slope in Lutz Ravine. The semi-deciduous forest canopy in the area is *c.* 35–40 m high. Mean leaf area index is about 7, with considerable spatial and seasonal variability (Leigh 1999; R. Wirth, B. Weber & R. J. Ryel, unpubl. data). For a detailed description of the forest see Foster & Brokaw (1982).

Measurement sites

Light measurements were taken at 16 sites in the understorey, where understorey was defined as sites having a canopy directly above them. The positions for the measurements were visually selected to cover a wide range of light situations in the understorey with respect to (1) canopy openness, (2) mean canopy height, (3) distance to vegetation and (4) the amount of reflected light.

Direct light measurements

Direct light (photosynthetic photon flux density, PPFD) measurements were taken at 16 sites in the understorey for 9 mo (February 1997–October 1997). Sensors were mounted horizontally 80 cm above the ground on PVC poles. Three quantum sensors (LI-190SB, LI-COR, Lincoln, Nebraska, USA) and 13 gallium arsenide phosphide photodiodes (Hamahatsu G1118, Hamahatsu, Middlesex, New Jersey, USA; Pearcy 1989) embedded in custom-made mounts were used. Low-cost gallium arsenide phosphide sensors have a good quantum response, with sharp cut-offs near 400 and 700 nm. All sensors and diodes were calibrated at the beginning and at the end of the study against a LI-COR quantum sensor that was recently calibrated by the company. For photodiodes, the slope of the calibration shifted by up to 30%, and hence we calculated a calibration factor for each month assuming a linear decrease of sensitivity. Shift of the quantum sensors was negligible.

Readings were taken automatically every 5 s, and averages over 1 h were stored by two data loggers (CR10X, Campbell Scientific, Inc., Logan, Utah, USA and LI-1000, Li-COR, Lincoln, Nebraska, USA). Daily integrals were calculated, including measurements from 06h00 to 20h00. The sensors were frequently checked for their horizontal position and for fallen debris.

Above canopy measurements were collected with a quantum sensor about 200 m south of the measuring sites atop a 42-m tower which reached above the canopy.

Hereafter, we will treat the light intensities derived from direct measurements as ‘reference’ values, keeping in mind, however, that a 10–25% error may be attached to these measurements under field conditions, due to spectral and cosine errors, and other technical limitations (Biggs 1986, Pearcy 1989, Mitchell & Whitmore 1993).

The long-term medians of the integrated daily light intensities at the measuring sites were between 0.237 and 2.895 mol m^{-2} d^{-1} (13-fold variation, Figure 1) and were between 0.67 and 8.14% of the light reaching the top of the canopy.

Indirect light measurements

Indirect light measurements were taken above each light sensor using (1) hemispherical photographs, (2) a LAI-2000 Plant Canopy Analyzer, (3) 38-mm digital photographs, (4) 24-mm photographs, (5) a spherical densiometer. Hemispherical photographs and plant canopy analysis recordings were taken at the beginning of each month from February to October 1997 and at the end of October; 38-mm photographs were taken monthly from June through October 1997; and 24-mm photographs and densiometer readings were taken once in February and April 1997, respectively.

All indirect measurements were only taken during uniformly overcast sky conditions or after sunset (mostly after 1700 h). All measuring devices were levelled and adjusted for magnetic north.

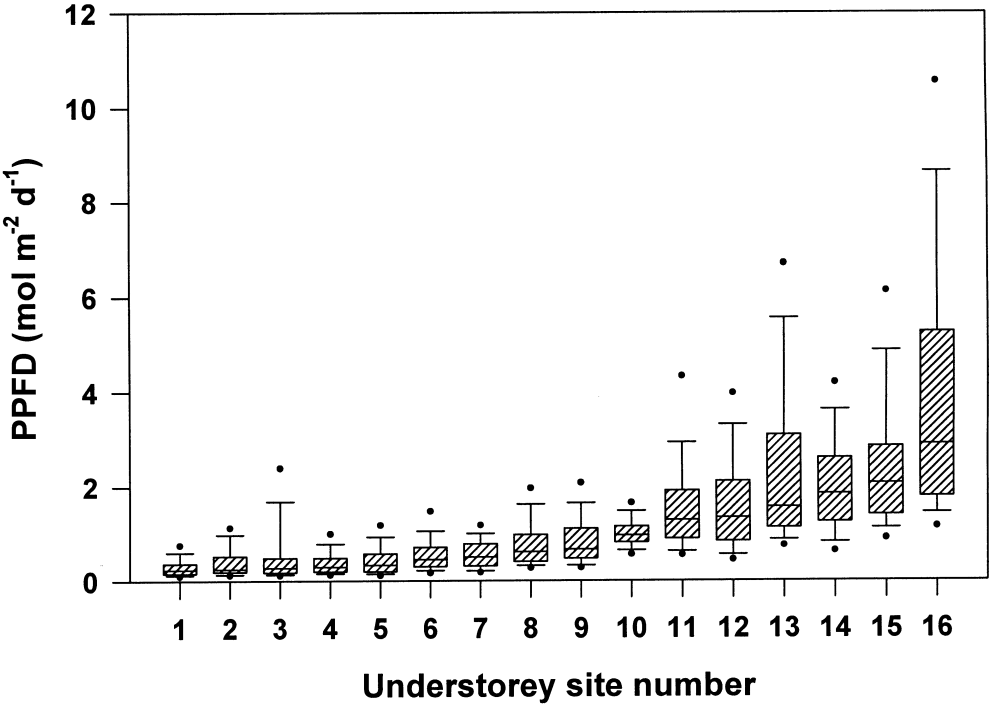

Figure 1. Daily integrals of PPFD for the 16 understorey sites on Barro Colorado Island, Panamá, that were continuously measured for 9 mo. The values in the Tukey-box plot are the medians, quartiles, the 10th and 90th percentiles and the 5th and 95th percentiles. For each site 206 to 270 daily light integrals were obtained.

Hemispherical fisheye photographs

Hemispherical fisheye photographs (hemiphotographs) were taken with a Nikkor 8-mm hemispherical lens (Nikkor) and a Nikon FM2 camera (Nikon, Melville, New York, USA) using Kodak Tri-X film (400 ASA, Eastman Kodak, Rochester, New York, USA). To enhance the contrast between openings and adjacent vegetation, the built-in red filter of the lens (R 60) was used. The camera was mounted on a monopod up to 10 cm above and 10 cm north of the sensors. Exposure time was 1/125 s and two photographs with aperture 4 and 5.6 (or 2.8 in very dark situations) were taken at each site. The photo with the best contrast was chosen for analysis.

Negatives of hemiphotographs were analysed using the computer software CANOPY (Rich 1989). The macro lens attached to the video camera was set at aperture 8. For all other specifications of the CANOPY system see Rich (1989). Every photograph was analysed at least twice, until the difference in direct site factor between two analyses was less than 10%. We arbitrarily chose to use the higher result for further computation. The hemispherical photographs were analysed for *direct site factor* (DSF), and *indirect site factor* (ISF). DSF and ISF refer to the photographic estimations of the proportion of direct and diffuse light levels under a canopy relative to the levels outside the canopy, respectively (Anderson 1964). Total proportion of light (*global site factor*, GSF) reaching a site was calculated as

$$\mathrm{GSF} = (\mathrm{ISF} + \mathrm{DSF}) / 2 \quad (1)$$

(Canham *et al.* 1990). Calculations for the site factors always refer to the whole year average.

Plant canopy analysis

Measurements with the LAI-2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, Nebraska, USA; Welles & Norman 1991) were taken with two optical sensors, each one attached to a separate control unit. Readings with the optical sensors were taken in the understorey (the 'below-canopy-sensor') and on the nearby tower above the canopy (the 'above-canopy-sensor'). Before each monthly measurement the two optical sensors were matched for equal readings. With the 'below-canopy-sensor' we took three instantaneous readings directly beside each diode or quantum sensor from different directions. The 'above-canopy-sensor' was mounted on a tripod and the control unit was set to continuous logging of readings every 15 s and high resolution, while measurements were taken in the understorey.

The LAI-2000 provides a measure of the fraction of sky visible to the 'below-sensor', the *Diffuse-Non-Interceptance* (DIFN). For the calculation of DIFN the procedures described in the manual were followed and the average of the three readings at each site was used.

Wide-angle photographs: 38 mm

At each site, 38-mm photographs were taken with a digital still camera (Sony DKC-ID1, Sony Corporation, Japan). The camera was placed on a monopod not more than 10 cm north of the sensors with the lens facing straight up. The upper side of the camera was adjusted for magnetic north, so that the width of the frame of view was stretching from east to west following the apparent solar path. The camera settings were the same for all pictures: normal resolution (resulting in 150 345 pixels), and maximal wide angle (f = 5.4 mm, which is equivalent to f = 38 mm on a regular 35-mm camera). The picture brightness was always set to an 'exposure value' of −1.5, to enhance contrast between foliage and openings (a setting between −2 and −1 yielded the most consistent results in tests preceding the measurements). Exposure time and aperture were then set automatically by the camera. Images were analysed with the software Adobe Photoshop, Tryoutversion (Adobe Systems Inc., San Jose, California, USA) following a standard protocol: (1) change of the data type of the image from colour to grey, (2) setting the 'contrast' of the image to '+100' and its 'brightness' to '−100'. The resulting image consisted only of black and white pixels, representing foliage and openings respectively. (3) The percentage of white pixels in the image was determined using the 'histogram option'.

Wide-angle photographs: 24 mm

Photographs were taken with a regular SLR camera (Ricoh KR-10, Ricoh Comp. West Caldwell, New Jersey, USA) with a 24-mm lens (Tokina 2.8/24mm, Tokina Industrial Inc., Medford, New York, USA) using Kodak Tri-X film (400 ASA, Eastman Kodak, Rochester, New York, USA). To enhance contrast between foliage and sky, red transparent foil was used as a filter (Pearcy 1989). Placing and orientation of the camera for taking the pictures followed the same method as described for 38-mm photographs. Two pictures were taken for each site, using a fixed exposure time (1/125 s) and two different apertures ($f = 4$ and $f = 5.6$ or $f = 2.8$). The negative with the best contrast was chosen for further analysis. The negatives were scanned with a Polaroid Slide Scanner (Sprint Scan 35, Polaroid Corp. Cambridge, Massachusetts, USA), using the following settings: 337 dpi, greyscale, BW negative and automatic exposure. The resulting images were processed and analysed as with the 38-mm photographs (see above) to obtain the percentage white pixels.

Spherical densiometer

'Canopy openness' as a measure of light, was estimated using a spherical densiometer, a concave mirror with an engraved grid system (Lemmon 1957). Four readings of canopy openness were made above each sensor from four different directions. The densiometer was hand-held at elbow height. The average of the readings was used as an index for canopy openness. Estimations were made by two people on two consecutive days: one person was experienced at using the device, the other was doing the estimations for the first time. The results of both persons were highly correlated ($df = 15$, $r = 0.90$, $P < 0.0001$).

Data analysis

We used least square regression to compare the data from indirect methods for measuring light conditions with directly measured long-term light levels. The relationship between short-term light measurements over individual days or weeks and long-term data was also assessed using regression analysis. Variance of the data was normalized by logarithmic transformation of the data prior to the regression analysis.

The daily integrals of the directly measured light in the understorey (mol photons m^{-2} d^{-1}) were averaged over the entire 9-mo period. Data were not available for some days due to technical problems, thus averages are for 206 to 270 days for each site.

The indirect methods yielded relative measures of light penetrating to the understorey from projections of the canopy: hemiphotographs: DSF, ISF and GSF; plant canopy analysis: DIFN; 38-mm and 24-mm photographs: % white pixels; and spherical densiometer: canopy openness.

From the output of the hemiphotographs we calculated absolute daily light flux in the understorey ($PPFD_{u\text{-}calc}$) as:

$$PPFD_{u\text{-}calc} = SF_{calc} \bullet PPFD_{a\text{-}meas} \tag{2}$$

where the relative light intensity in the understorey (SF_{calc}) is expressed as DSF, ISF or GSF, and $PPFD_{a\text{-}meas}$ is the 9-mo average of integrated daily light flux measured above the canopy.

Plant canopy analysis measurements and wide-angle photographs do not provide absolute light values. DIFN and % white pixels were therefore correlated with the directly measured proportion of light reaching the understorey (SF_{meas}):

$$SF_{meas} = PPFD_{u\text{-}meas} / PPFD_{a\text{-}meas} \tag{3}$$

To assess the accuracy of the indirect methods for estimating light conditions in the understorey, we determined the error (E) of the indirect, calculated estimates ($V_{u\text{-}calc}$) as a percentage of the directly measured light conditions ($V_{u\text{-}meas}$) at each site as

$$E_{site} = | (V_{u\text{-}meas} - V_{u\text{-}calc}) / V_{u\text{-}meas} | \bullet 100 \tag{4}$$

and the error as a percentage of the full range of light conditions under consideration, as:

$$E_{range} = \frac{| V_{u\text{-}meas} - V_{u\text{-}calc} |}{\text{maximum } V_{u\text{-}meas} - \text{minimum } V_{u\text{-}meas}} \bullet 100 \tag{5}$$

For the calculation of errors, the proportion of light reaching the understorey (SF_{calc}) was calculated using the equation of the regression between direct light measurements and the data output from the plant canopy analysis measurements and from 38-mm photographs (V stands for DIFN or % white pixels):

$$\log SF_{meas} = a + b \bullet \log (V) \tag{6}$$

as:

$$SF_{calc} = 10^{a} \bullet V^{b} \tag{7}$$

Several sampling schemes (Table 1), corresponding to those employed in previous studies, were used to calculate light levels from the indirect estimates. To that end, we either used (1) indirect measurements from each month for each site (entire data sets) or we picked different subsamples: (2) only measurements at the beginning and the end of the study, (3) only measurements from one month, or (4) only measurements from one month for each site, but measurements at different sites were taken at different times. For the schemes (3) and (4) we repeated the analysis for each month, or for 10 random combinations of the monthly measurements, respectively (see Table 1 for further explanations).

We also picked different subsets of the direct light measurements to simulate short-term light measurements and related them to the long-term direct measurements.

Table 1. Description of four sampling schemes that were used for calculation of light conditions from indirect methods.

	Method	Sampling scheme			
		1 Monthly average	2 Average of endpoint	3 Single month, all sites simultaneously	4 Single month, not simultaneously for all sites
			→ Decreasing effort and expense		
Description of sampling scheme		Every month at each site	At the beginning and the end of a study	Only once at each site all simultaneously	Only once at each site, each site at a different time
Number of measurements per site		10 (6)	2	1	1
Measurements included in calculations and number of data sets for regressions	Hemi-photographs	All 10 monthly measurements	February and end-October measurements	Each set of monthly measurements separately	A random combination of monthly measurements
		(1 data set)	(1 data set)	(10 data sets)	(10 data sets)
	Plant canopy analysis	All 10 monthly measurements	February and end-October measurements	Each set of monthly measurements separately	A random combination of monthly measurements
		(1 data set)	(1 data set)	(10 data sets)	(10 data sets)
	38-mm photographs	All 6 monthly measurements	June and end-October	Each set of monthly measurements separately	A random combination of monthly measurements
		(1 data set)	(1 data set)	(6 data sets)	(10 data sets)
	Direct for a week	1st week of each month	1st week in February and last week in October	A randomly chosen single week	A random combination of different weeks
		(1 data set)	(1 data set)	(10 data sets)	(10 data sets)
	Direct for a day	1st day of each month	1st day in February and last day in October	A randomly chosen single day	A random combination of different days
		(1 data set)	(1 data set)	(10 data sets)	(10 data sets)
	24-mm photographs	—	—	February (1 data set)	—
	Spherical densiometer	—	—	April (1 data set)	—

Regression coefficients (r^2) and the equations of the regressions were calculated using Excel (Excel 97, Microsoft Corp., Seattle, USA). P-values were calculated using InStat (Graph Pad Software, USA). For schemes 3 and 4 we compared the methods and schemes, by comparing the regression coefficients in an ANOVA (DataDesk, Data Description Inc. Ithaca, USA). Errors were compared with a Kruskal–Wallis test in Statistica (StatSoft Inc., Tulsa, Oklahoma, USA).

RESULTS

Light estimates calculated from three of the indirect methods, hemiphotographs, plant canopy analysis readings and 38-mm photographs, all showed a highly significant relation to directly measured light conditions in the understorey (Figure 2, Table 2). For hemiphotographs, the regression line between measured and calculated absolute light values was close to 1:1. DSF always yielded the best results, compared to ISF or GSF (data not shown). Plant canopy analysis measurements and 38-mm photographs do not result in estimates of absolute light levels, but in estimates of canopy structure (DIFN and % white pixels, respectively) that are closely related to the proportion of light reaching the understorey. Values of r^2 were greatest for the plant canopy analysis, however, differences of the goodness of fit among these three methods were slight and only significant in the case of simultaneous sampling (scheme 3, ANOVA: $P < 0.0005$).

The errors resulting when estimating light from the indirect methods using average-of-endpoints sampling (scheme 2) are shown in Figure 3. Calculations using the other sampling regimes resulted in the same range of errors (data not shown). When relating the difference between the directly measured and the calculated values to the long-term average light conditions of the respective sites (E_{site}), a considerable error occurred for all methods (Figure 3a). Estimates for more than half of the sites deviated by more than 20, 25 and 40% from the direct measurements for hemiphotographs, plant canopy analysis and 38-mm photographs, respectively. However, when relating the difference to the range of the light conditions under consideration (E_{range}), the error was much lower for all methods, with medians of about 5% and maximum values of 40% (Figure 3b). The accuracy of the methods was significantly different for E_{site} (Kruskal–Wallis test: $P < 0.05$), but not for E_{range}. There was no trend towards higher errors at low understorey light conditions.

Short-term direct light measurements for a week or a day also were highly significantly related with light intensities over the entire 9-mo measuring period (Table 2). In contrast, estimates of canopy openness with a spherical densiometer showed only a weak relation to light intensities in the understorey. The calculation models, representing different sampling schemes, differed only slightly in their ability to predict long-term light conditions in the understorey (Figure 2, Table 2). For the plant canopy analysis and 38-mm photographs,

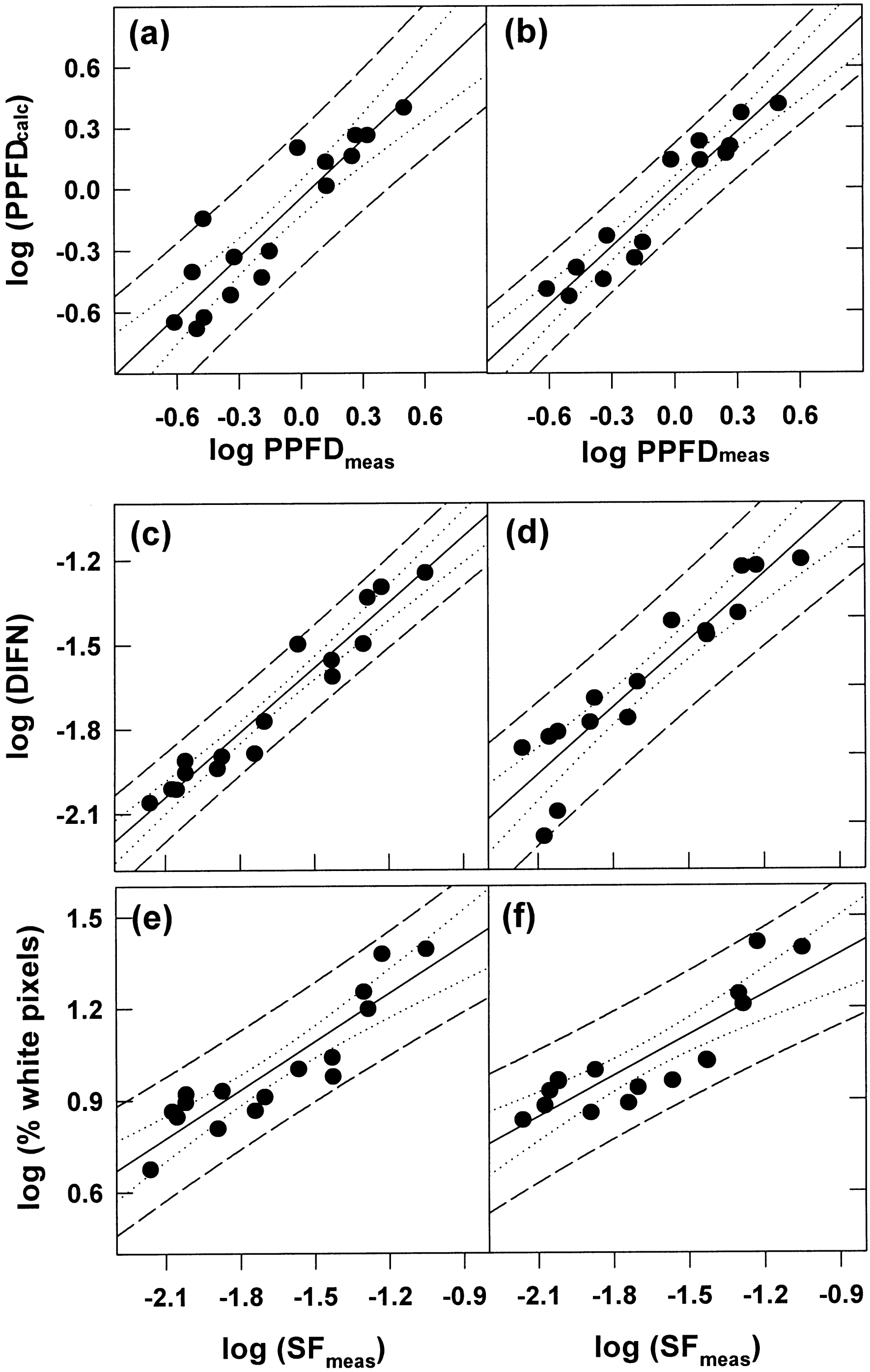

Figure 2. Regression between direct measurements of light conditions and indirect estimates calculated from hemispherical photographs (a, b), plant canopy analysis (c, d) and 38-mm digital photographs (e, f) using scheme 1 (a, c, e) and 2 (b, d, f), including the 95% confidence intervals (dotted lines) and the prediction intervals (broken lines).

For hemiphotographs the measured absolute daily PPFDs ($PPFD_{meas}$) were related to absolute daily PPFDs values calculated from DSF ($PPFD_{calc}$). For the plant canopy analysis and 38-mm photographs, the measured proportion of light (SF_{meas}) was related to the indirect measure (DIFN and % white pixels, respectively). The equations of the regressions are (a): $y = 0.955x - 0.045$; (b): $0.939x - 0.005$; (c): $y = 0.768x - 0.429$; (d): $y = 0.975x - 0.137$; (e): $y = 0.527x - 1.882$; (f): $y = 0.445x - 1.779$. $P < 0.0001$ for all regressions, for r^2 values see Table 2.

Table 2. Values of r^2 for regressions of five indirect estimates and two short-term direct measures with long-term direct light measurements. For schemes 3 and 4 the data are the mean ± SD. Minimum and maximum r^2-values and the number of regressions are given in parentheses. The regressions (scheme 1 and 2) and the means of the regression coefficients (scheme 3 and 4) were highly significant ($P < 0.0001$), except for 'direct for a day – scheme 4' ($P < 0.005$) and 'spherical densiometer' ($P < 0.05$). For schemes 3 and 4 the regressions with the lowest fit were always still significant at least at the 90% level.

Method	Sampling scheme			
	1 Monthly average	2 Average of endpoint	3 Single month, all sites simultaneously	4 Single month, not simultaneously for all sites
Hemiphotographs (DSF)	0.83	0.92	0.75 ± 0.09 (0.59–0.84; n = 10)	0.67 ± 0.11 (0.51–0.85; n = 10)
Plant canopy analysis	0.94	0.87	0.91 ± 0.05 (0.78–0.94; n = 10)	0.72 ± 0.08 (0.56–0.82; n = 10)
38-mm photographs	0.82	0.74	0.76 ± 0.09 (0.64–0.87; n = 6)	0.72 ± 0.08 (0.56–0.82; n = 10)
Direct for a week	0.98	0.90	0.88 ± 0.06 (0.73–0.95; n = 10)	0.79 ± 0.11 (0.59–0.89; n = 10)
Direct for a day	0.96	0.94	0.82 ± 0.15 (0.55–0.96; n = 10)	0.63 ± 0.13 (0.44–0.83; n = 10)
24-mm photographs	—	—	0.79 (n = 1)	—
Spherical densiometer	—	—	0.37 (n = 2)	—

using measurements from all months (scheme 1) yielded slightly higher r^2-values than including only the average-of-endpoint samples. For sampling schemes with only one measurement for each site, taking all measurements simultaneously (scheme 3) generally improved the relation compared to taking them at different days for each site (scheme 4). For the plant canopy analysis, week-long, and day-long direct measurements this difference was significant ($P < 0.001$, $P < 0.05$ and $P < 0.01$, respectively). Although for scheme 3 the average fit was almost as high, as in scheme 1 and 2, r^2 varied considerably between measuring dates. The respective smallest r^2, although still significant, was very low, e.g. for hemiphotographs the lowest r^2 was only 0.59 (Table 2).

Week-long direct measurements every month (scheme 1) were very tightly related to continuously measured light intensities (Table 2). This is not surprising, since data of almost one-quarter of the study period were included. Day-long direct measurements for one day each month also yielded a surprisingly good fit. However, when only light values measured in one week or on one day were taken into consideration, the r^2 varied considerably depending on the actual week or day included, and the lowest fit was fairly weak, especially for the single day measurements (Table 2). Additionally, between regressions for measurements from different days, there was a very high variation of the y-intercept (coefficient of variation: >5000). Combining day-long measurements from different times for the different sites therefore resulted in r^2 values, which were significantly lower than for all other methods and sampling schemes (ANOVA: $P < 0.005$; Scheffé post-hoc test).

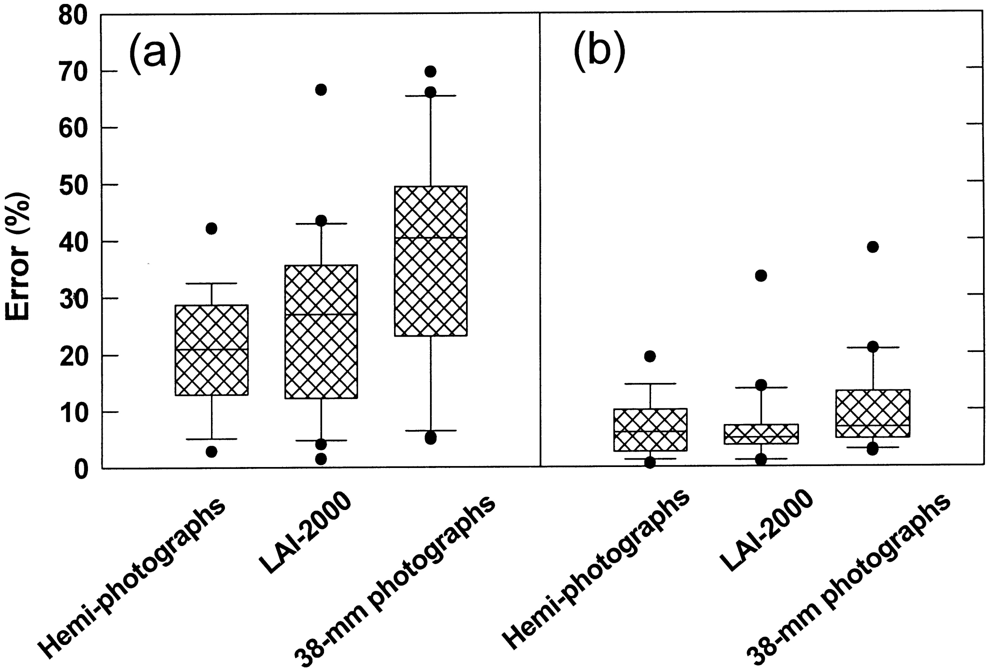

Figure 3. Errors of calculated light values for three indirect methods. In (a) errors are calculated relative to the individual value for each site, in (b) errors are calculated relative to the range of means of light conditions encountered at the 16 sites (see Eqns 4 and 5). For hemiphotographs, directly measured and calculated absolute light intensities were used. For plant canopy analysis (LAI-2000) and 38-mm photographs SF_{calc} was calculated from the transformed equation of the regression of SF_{meas} on the data output (see Eqns 6 and 7). The equations were (1) $SF_{calc} = 1.271 \times DIFN^{0.888}$ and (2) $SF_{calc} = (4.091 \times 10^{-4}) \times (\% \text{ white pixels})^{1.657}$. Tukey-box plot as in Figure 1, except that outliers are shown instead of the 5th and 95th percentiles.

DISCUSSION

Estimates from the indirect methods hemiphotographs, plant canopy analysis and 38-mm photographs to quantify light conditions all yielded a good fit with directly measured long-term PPFD in the understorey of a tropical forest. Only estimates of canopy openness from a spherical densiometer showed a weak relation to light conditions at the measuring sites.

Estimates from hemiphotographs can directly be converted into absolute light intensities if above-canopy PPFD is known, and calculated values showed no bias towards higher or lower values (Figure 2 a,b). Estimates from the plant canopy analysis and the wide-angle photographs have to be transformed to yield the actual proportion of light in the understorey. Incorporation of above-canopy light measurements can then yield absolute light values even from these methods.

The analysis of the errors of the calculated values showed that they are large when related to single site light measurements, but relatively small when related to the range of measured light conditions in the understorey. This means that all three methods give a reliable ranking of light conditions when working in a relatively large number of sites, even within the range of low understorey light intensities. This is due to the fact that light conditions in the understorey still vary up to 20-fold. However, the indirect methods are not suited to predict light conditions accurately for single sites. Direct light measurements are still the only means to achieve this goal, because their inherent error is much smaller (10–25% relative to *single* measurements; Pearcy 1989). For each particular study the method has to be carefully matched to the accuracy needed: indirect estimations of light are useful in large-scale ecological studies, e.g. to relate growth of large numbers of plants to light conditions at their microsite, or to compare landscape-scale light conditions between forests. They are not suited for physiological studies where accurate average light conditions or even short-term light dynamics are of importance.

The fit of estimates from the indirect methods with the long-term light conditions at different microsites in the understorey was surprising. Comparisons of indirect methods with direct light measurements have so far mainly focused on much higher gradients of light, i.e. gaps of different sizes, or gaps versus understorey. The generally few values taken in the dark forest understorey suggested poor applicability of the methods in this habitat (Becker *et al.* 1989, Chazdon & Field 1987, Easter & Spies 1994, Rich *et al.* 1993, Roxburgh & Kelly 1995, Whitmore *et al.* 1993). Machado & Reich (1999) recently found plant canopy analysis, but not hemispherical photographs, to be suitable to assess understorey light conditions in conifer forests.

In this study in a semi-deciduous tropical forest, the empirical relations held despite a number of theoretical problems with the methods when applied in the understorey. These especially concern the inability of the methods to pick up light which has been reflected by plant parts, or to account for penumbral effects (see Mitchell & Whitmore (1993) for a detailed discussion for hemiphotographs). These problems, on the other hand, undoubtedly are at least part of the reason that single site light conditions could not be predicted without considerable error. The measurement error involved in the direct light measurements themselves also contributes to the deviation of predicted from measured values.

Surprisingly, even for 38-mm wide-angle photographs analysed with regular photo-editing software, the empirical data yielded almost as good results as the much more sophisticated methods. This was probably due to the fact that in closed tropical forests the highest proportion of both direct and indirect light is most likely to penetrate canopy openings within only a small angle around the zenith. This is because (a) the probability is higher that there is an opening unobscured by leaves or branches directly above (the path of a light beam through the canopy is relatively shorter) and (b) in the tropics the apparent path of the sun passes close to the zenith all year. The close fit observed in this study using 38-mm photographs may therefore only hold for closed-canopy situations of tall, evergreen or semi-deciduous tropical forests. We suggest the method has a high potential for use in other tropical forests, but its universal applicability remains to be tested. Tests are worthwhile, because the method has the advantage of low price and fast data-processing (see Table 3). It should be kept in mind, however, that these photographs, in contrast to hemispherical photographs and plant canopy analysis measurements do not allow any further conclusions about canopy structure.

When only direct light measurements from a week or even a day were included in the analysis, we still yielded highly significant regressions with the long-term light data. Thus, short-term direct light measurements offer another powerful means to rank long-term light conditions at different microsites in the understorey. Single-day measurements cannot be successfully used to estimate absolute long-term light intensities, because the y-intercept of the regression strongly depends on the period when the measurements were actually taken. However, this difficulty can be overcome by repeatedly taking single-day measurements throughout the measuring period.

Different calculation schemes yielded a similar goodness of fit. The schemes correspond to different sampling schedules, that include vastly different sampling effort, with the effort and expense decreasing from scheme 1 through 4. The highest goodness of fit was obtained when applying the different indirect methods either monthly or at the beginning and the end of the study period (scheme 1 and 2).

Taking indirect measurements every month generally enhanced the accuracy compared to taking measurements only once or twice, but goes along with a considerable increase in sampling effort. Including endpoint data did not (or only slightly) improve the fit with direct measurements compared to the average of goodness of fit from a single month (scheme 3). However, the minimum regression coefficient was quite low, suggesting the risk for a high error involved when taking measurements only once. Taking measurements at each site at a different day (scheme 4) further increased the error. However, even here regressions were always significant, suggesting that it might still be suitable, when practical considerations require this sampling scheme and the scope of the study allows for relatively low accuracy. Sampling twice, at the beginning and the end of a study, offers a good compromise between accuracy and sampling effort (Anderson 1964).

The study showed that a number of indirect methods are well suited to rank long-term light intensities at sites within the understorey of tropical forests, and therefore offer a cheaper and less labour-intensive alternative to long-term direct light measurements for a number of studies. Which method is used, can primarily be decided by practical and financial considerations, rather than differences in the accuracy of the methods. In Table 3, we summarize a number of advantages and disadvantages of the methods.

The study also showed that none of the indirect methods or short-term direct measurements predict light conditions for single sites in the understorey with

Table 3. List of practical aspects of indirect methods to estimate understorey light conditions of tropical forests. +, positive; –, negative.

	Hemispherical fisheye photographs[1]	Plant canopy analysis	38mm - wide angle photographs[2]	Short-term direct measurements
Data collection (field)	+ no requirement for open areas	– requires open area or above canopy access	+ no requirement of open areas	+ no requirement of open areas
	+ can be used whenever the lens is not in direct sunlight	– can only be used under uniformly illuminated skies (often less than 1 hour per day)	+ can be used whenever the lens is not in direct sun	+ can be used under all weather conditions
	+ can be used in light rain	– cannot be used in rain	+ can be used in light rain	
Time requirement in the field	+ low	– high	+ low	– high
	+ no work other than at measuring sites	– requires setup and removal of 'above-canopy sensor'	+ no work other than at measuring sites	– time consuming set up, checks and removal
	+ time requirement at every site low	– time requirement at every site slightly higher	+ time requirement at every site low	
Data processing (lab)	– development of negatives, digitizing of negatives, setting of threshold, analysis	+ requires only data downloading and computing	+ requires data downloading, simple analysis	+ requires only data downloading
	+ good possibility to check for and correct image quality	– limited possibility to check data quality	+ possibility to check image quality	+ measuring errors unlikely
	– determination of threshold subjective[3], data from independent projects almost not comparable	+ if handled accurately, results are independent of who handles equipment	+ if handled accurately, results are independent of who handles equipment	+ results are independent of who handles equipment

Table 3. (*cont.*)

	Hemispherical fisheye photographs[1]	Plant canopy analysis	38mm - wide angle photographs[2]	Short-term direct measurements
Time requirement in lab	– high	+ very low	+ low	+ very low
Costs	– moderately high	– high	+ low	variable
Main sources of error	• setting of threshold and differences in light conditions	• non-uniform sky conditions	• canopy openings to the side	• variable relationship with long-term values
Main advantages	• good usability in remote sites[4] • usable in wide range of weather conditions • possibility to check quality • gives further information	• good accuracy • fast data processing • also gives LAI	• cheap • easy • fast	• some equipment often available
Main disadvantages	• subjective setting of threshold • time consuming data analysis	• narrow time window with adequate illumination • limited possibility to check measurement	• potentially only valid in the understorey of tall tropical forests • validity remains to be shown for other forests	• cannot be calibrated against absolute PPFD • not practical in large number of sites • time consuming

[1] Based on the usage of SLR-camera, a digital camera can be used instead.
[2] Based on the usage of a digital still camera. An SLR camera can be used instead. Then slides have to be digitized for analysis.
[3] Coordination of collaborating people is possible.
[4] Does not depend on electricity nor immediately available computer facilities.

an error that is reliably less than 30%. Therefore, none of the simplified, indirect methods are an option when accurate single site light intensities have to be assessed.

ACKNOWLEDGEMENTS

We thank the Smithsonian Tropical Research Institute, Panamá, for giving us the opportunity to work at Barro Colorado Island. Equipment to conduct this comparison of methods was made available by W. Beyschlag, J. Wright, S. Paton, R. Ríos, the Smithsonian Environmental Science Program and the Smithsonian Tropical Research Institute. Above-canopy light measurements are courtesy of the Smithsonian Environmental Science Program. Z. Maynard did one set of densiometer measurements. C. Lovelock, T. Kursar and E. Leigh gave valuable comments on the manuscript. Thanks for the encouragement to do this work are due to E. Leigh, D. and D. Clark and U. Lüttge. This work was supported by the Deutsche Forschungsgemeinschaft.

LITERATURE CITED

ANDERSON, M. C. 1964. Studies of woodland light climate. I. The photographic computation of light conditions. *Journal of Ecology* 52:27–41.

BECKER, P., ERHARDT, D. W. & SMITH, A. P. 1989. Analysis of forest light environments. Part I. Computerized estimation of solar radiation from hemispherical canopy photographs. *Agriculture and Forest Meteorology* 44:217–232.

BIGGS, W. 1986. Radiation measurement. Pp. 3–20 in Gensler, W. G. (ed.). *Advanced agricultural instrumentation*. Nijhoff, Dordrecht.

CANHAM, C. D., DENSLOW, J. S., PLATT, W. J., RUNKLE, J. R., SPIES, T. A. & WHITE, P. S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20:620–631.

CHAZDON, R. L. & FETCHER, N. 1984. Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. *Journal of Ecology* 72:553–564.

CHAZDON, R. L. & FIELD, C. B. 1987. Photographic estimation of photosynthetically active radiation: evaluation of a computerized technique. *Oecologia* 73:525–532.

DENSLOW, J. S., SCHULTZ, J. T., VITOUSEK, P. & STRAIN, B. R. 1990. Growth responses of tropical shrubs to treefall gap environments. *Ecology* 71:165–179.

EASTER, M. J. & SPIES, T. A. 1994. Using hemispherical photography for estimating photosynthetic photon flux density under canopies and in gaps in Douglas-fir forests of the Pacific Northwest. *Canadian Journal of Forest Research* 24:2051–2058.

ENDLER, J. A. 1993. The color of light in forests and its implications. *Ecological Monographs* 63:1–27.

ENGELBRECHT, B. M. J. 1998. *. . . wo der Pfeffer wächst . . . , Ökologie und Ökophysiologie von koexistierenden Piper-Arten im Unterwuchs tropischer Regenwälder*. Dissertation. Universität Darmstadt. 147 pp.

FOSTER, R. B. & BROKAW, N. V. L. 1982. Structure and history of the vegetation of Barro Colorado Island. Pp. 67–81 in Leigh, E. G., Rand, A. S. & Windsor, D. M. (eds). *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, DC.

LEMMON, P. E. 1957. A new instrument for measuring forest overstory density. *Journal of Forestry* 55:667–668.

LEIGH, E. G. 1999. *Tropical forest ecology. A view from Barro Colorado Island*. Oxford University Press, New York. 245 pp.

MACHADO, J.-L. & REICH, P. B. 1999. Evaluation of several methods of canopy openness as predictors of photosynthetic photon flux density in deeply shaded conifer-dominated forest understorey. *Canadian Journal of Forest Research* 19:1438–1444.

MITCHELL, P. L. & WHITMORE, T. C. 1993. Use of hemispherical photographs in forest ecology: calculation of absolute amount of radiation beneath the canopy. *OFI Occasional Papers* 44. Oxford Forestry Institute. 39 pp.

PEARCY, R. W. 1989. Radiation and light measurements. Pp. 97–116 in Pearcy, R. W., Ehleringer, J., Mooney, H. A. & Rundel, P.W. (eds). *Plant physiological ecology: field methods and instrumentation*. Chapman and Hall, New York.

RICH, P. M. 1989. A manual for analysis of hemispherical canopy photography. *Los Alamos National Laboratory Technical Report* LA-11733-M. Los Alamos, New Mexico. 80 pp.

RICH, P. M., CLARK, D. B., CLARK, D.A. & OBERBAUER, S.F. 1993. Long-term study of solar radiation regimes in a tropical wet forest using quantum sensors and hemispherical photographs. *Agriculture and Forest Metereology* 65:107–127.

ROXBURGH, J. R. & KELLY, D. 1995. Uses and limitations of hemispherical photography for estimating forest light environments. *New Zealand Journal of Ecology* 19:216–217.

SMITH, A. P., HOGAN, K. P. & IDOL, J. R. 1992. Spatial and temporal patterns of light and canopy structure in a lowland tropical moist forest. *Biotropica* 24:503–511.

WHITMORE, T. C., BROWN, N. D., SWAINE, M. D., KENNEDY, D., GOODWIN-BAILEY, C. I. & GONG, W.-K. 1993. Use of hemispherical photographs in forest ecology: measurement of gap size and radiation totals in a Bornean tropical forest. *Journal of Tropical Ecology* 9:131–151.

WELLES, J. M. & NORMAN, J. M. 1991. Instrument for indirect measurement of canopy architecture. *Agronomy Journal* 83:818–825.