Ann. For. Sci. 58 (2001) 877–891

Original article

A comparison of five indirect methods for characterizing the light environment in a tropical forest

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(Received 23 August 2000; accepted 6 September 2001)

Abstract – We compared five methods for measuring light availability in the tropical forest understorey: the LAI-2000 PCA, an empirical LAI-metre, a densiometre, photosensitive diazo paper metres, and hemispherical photographs. Measurements were made along three 250 m transects and adjacent to 95 seedlings on four logged or virgin plots of a French Guianese forest. Correlation analysis showed that more mobile and less expensive methods, such as the LAI metre and diazo paper metres, can provide similar information to more cumbersome or expensive equipment such as the LAI-2000 metre or hemispherical photographs. All instruments except the densiometre detected differences among seedlings from different post-logging microsites. Few significant correlations were found between light measures and the number of trees or their basal area within 10 m, which may reflect an increase in the density of smaller stems and lianas during post-logging succession.

light measure / tropical forest / leaf area index / seedling / hemispherical photography / diazo paper

Résumé – **Comparaison de cinq méthodes pour caractériser l'environnement lumineux de plantules en forêt tropicale.** Cinq méthodes de mesure de la quantité de lumière disponible dans le sous-bois d'une forêt tropicale sont comparées : le LAI-2000 PCA, un appareil de mesure empirique du LAI, un densiomètre, des papiers diazo photosensibles et un appareil de photographie hémisphérique. Les mesures ont été effectuées le long de trois transects de 250 m et à proximité de 95 plantules, dans quatre parcelles exploitées ou vierges d'une forêt guyanaise. L'analyse des corrélations entre mesures montre que des méthodes comme l'appareil de mesure empirique du LAI ou les papiers diazo peuvent fournir, de façon plus pratique et moins coûteuse, des informations semblables à celles données par le LAI-2000 ou les photographies hémisphériques. Tous les appareils, excepté le densiomètre, décèlent des différences entre des plantules poussant dans des microhabitats rendus différents par l'exploitation. Peu de corrélations significatives entre les mesures de lumière et l'effectif d'arbres ou leur surface terrière dans un rayon de 10 m ont été trouvées, ce qui tend à indiquer que la densité des petites tiges et des lianes s'est accrue à la suite de l'exploitation.

mesure de lumière / forêt tropicale / indice foliaire / plantule / photographie hémisphérique / papier diazo

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1. INTRODUCTION

Many factors have been demonstrated to influence the growth and survival of tropical tree seedlings, including biotic factors such as predation [39], herbivory [24], and pathogens [1], as well as abiotic factors including litter depth [30], soil moisture [42], soil nutrients [5], and physical damage [11]. However, to date the majority of studies of tropical tree regeneration have examined in some way the influence of light availability [49]. Indeed, differential responses among tropical tree species in the light requirements of seedlings have been proposed as a potential mechanism for the maintenance of species richness in tropical forest tree communities [22, 15].

Most experimental studies to date have focused on seedling response in shadehouses with varying degrees of light intensity [3, 36, 43], or have compared responses between understorey and light gap conditions [33], or among gaps differing in size [25, 31]. However shadehouse conditions do not adequately duplicate the light environments in the field [7, 8, 32], and gaps, although playing an important role in gap-phase regeneration, constitute a relatively small percentage of surface area [29]. Thus, a complete understanding of forest regeneration necessitates observations and experiments along the entire gradient from understorey to large gaps.

To date studies investigating light availability in the forest understorey have encountered difficulty in describing light environments [17]. We recognize four problems. First, many methods make only punctual measures, and thus may not capture the temporal variation of sunflecks received at a site [7, 44]. Second, local and fine-scale spatial variation obliges measurements to be made at increasingly finer spatial scales to adequately describe light availability for plots [32] or individual seedlings (Baraloto and Couteron, in prep.) Third, not only the quantity of light-energy, but also the quality (e.g. red/far-red ratio [8]) may be important, and few methods permit such measures. Finally, the feasibility of implementation may play a role in the choice of method. For example, a comparison of sites separated by large distances requires either punctual measures, or some type of mobile integrated measure. In addition, some methods require particular climatic conditions, and thus limit the possibility of conducting research during the rainy season. Eventually, many laboratories simply do not have access to the more expensive instruments.

In this paper we address these issues by comparing the relative merits of five methods for measuring light availability: the LAI-2000 Plant Canopy Analyzer, an empirical LAI-metre, a spherical densiometre, diazo papers and hemispherical photographs. The goals of the study were (1) to evaluate the instruments based on the consistency of their respective measurements; (2) to evaluate the instruments based on their ability to produce measures that do not vary for small variations in space or time; and (3) to determine the degree to which quantitative measures are correlated with stand differences and stand-based competition indices. We investigated both 12-year-old second-growth stands and unlogged stands, as these represent a more extensive gradient of light conditions.

2. MATERIALS AND METHODS

2.1. Study site

The measurements were performed in the Paracou experimental station, which is located 50 km west of Kourou in French Guiana (5° 15’ N, 52° 55’ W). The forest is seasonal moist tropical forest, receiving an average annual rainfall of 3160 mm. The relief consists of small hills (less than 50 m high) separated by wet areas, with medium slopes (30% maximum).

In 1984, 12 square plots of 6.25 ha each were delimited in the primary forest. From 1986 to 1988, the plots underwent three silvicultural treatments according to a randomized block design with 3 replicates: treatment 1 consisted of medium-intensity logging (about 10 logged trees per ha); treatment 2 consisted of medium-intensity logging ($\simeq$ 11 ha^{-1}) plus thinning by poison-girdling of noncommercial species ($\simeq$ 29 ha^{-1}); treatment 3 consisted of an intensive logging ($\simeq$ 29 ha^{-1}) plus thinning of noncommercial species ($\simeq$ 15 ha^{-1}); three plots were left untouched as controls. On each plot, all trees greater than 10 cm DBH (diameter at breast height) have been identified, mapped and measured annually from 1984 to 1995, and once every two years since. A more precise description of the Paracou experimental station is given by Schmitt and Bariteau [38].

2.2. Plant canopy analyzer

The LAI-2000 Plant Canopy Analyser (Li-Cor, Lincoln Inc., NE, USA) was used to assess the plant area index (*PAI*) and the diffuse non-interceptance (DIFN). The LAI-2000 PCA measures the diffuse sky radiation on five concentric annuli in the ranges 0–12°, 15–28°, 31–43°, 45–58° and 61–74° from zenith. A built-in optical filter rejects radiation above 490 nm, thus limiting the contribution of the light scattered by the foliage. From above- and below-canopy measurements, the LAI-2000 PCA computes the transmittance for each sky vector, and then inverts them into *PAI* or averages them into DIFN. The calculations, which are automatically derived by the built-in C2000 Li-Cor software [28], are based on four hypotheses: foliage is a black body that absorbs all the light it receives; light-blocking plant elements are randomly distributed in the canopy; plant elements have the same projection as simple geometrical convex shapes; plant elements are small compared to the area spanned by each ring.

2.3. Empirical LAI-meter (LAIL)

The empirical LAI-metre (LAIL PC4, CEA Saclay, France) [13] consists of a peep-hole lens, which can be assimilated to a lens spanning the range 0–90° from zenith, with a 4.5 mm photoresistor attached to the bottom. The photoresistor is sensitive to light in the PAR region, between 400 and 750 nm. It is connected to an ohmmeter. As the photoresistor absorbs photons from the light flux and emits electrons that increase its electric conductivity, its resistance is related to the amount of incident light. A second order polynomial relationship is used to link the logarithm of the resistance R (in kΩ) to the logarithm of the irradiance I. Its calibration implies a calibrated light source, neutral filters and a pyranometre (LI-200SB, Li-Cor, USA).

The *PAI* estimate relies on the Beer-Lamber law, that can be written as: $kPAI = -\ln I + \ln I_0$ where I is the below-canopy irradiance, I_0 is the above-canopy irradiance, and k is the extinction coefficient. An empirical correction factor C is used to account for I_0 and an average value of $k = 0.88$ that was previously determined at Paracou is used [13], so that the relationship between *PAI* and the resistance R writes as: $PAI = \alpha \ln R + \beta (\ln R)^2 + \gamma + C$. The parameters α, β and γ are specific to each instrument. For the one we used: $\alpha = 2.124$, $\beta = -0.101$ and $\gamma = 2.211$.

The correction factor C depends on the light conditions only, which are empirically assessed: when sun flecks are bright and shadows sharply outlined, $C = 0$; when sun flecks are pale and shadows still present, $C = -0.6$; when sun flecks are absent but shadows still visible, $C = -1.2$. The instrument should not be used under darker conditions, and cannot be used in open spots. The best measurements are achieved when the sun is at zenith, that is to say at solar soon ± 1.5 hours [13].

2.4. Spherical densiometre

The densiometre (Ben Meadows Company, Canton, GA, USA) consists of a convex spherical-shaped mirror with a reflection field of 45°, engraved with a grid of 24 squares [12, 17, 27]. The size of a square is a quarter inch. The instrument is held horizontally at waist height. Each square is mentally divided by four, and the number of square quarters in which the sky reflects is counted. Sky openness, defined as the percentage of sky not blocked by plant elements after projection on a hemisphere whose axis is vertical, is estimated from four measures made in orthogonal directions.

2.5. Hemispherical photographs

Another tool that provides an estimate of the sky openness is hemispherical photography [37, 45]. Like the LAI-2000 PCA, hemispherical photographs enable one to compute the *PAI* from gap fraction estimates in different zenithal and azimuthal ranges. We used a Nikon F601 camera with a Nikkor 10 mm fisheye lens which produces an orthographic projection, and Kodak TMY 400 ASA film. A height adjustable tripod was also used. Light conditions were determined using a Sekonic photoelectric cell. A red filter was used to enhance the contrast between the sky and the vegetation.

The films were developed using Kodak Microdol-X TM procedure and then digitized by the commercial Kodak PhotoCD service. The grey-scale images were outlined and processed into black and white bitmap images using Corel Photo Paint. The images were further processed using the Cimes package [45]. The LAI1 program was first used to compute the gap fractions in 18 zenithal annuli (from 0 to 90° with a 5° step) and 24 azimuthal sectors. The sky openness was then computed from the gap fractions by the Closure program, whereas the *PAI* was computed from the gap fractions by the LAIMLR (leaf area index after Miller-Lang) program. Both Closure and LAIMLR enable to restrict the input gap fractions to some central zenithal annuli. The calculations that they perform are based on the same hypotheses as the ones used by the LAI-2000 PCA.

2.6. Diazo papers

The diazo paper light metres [19] were made of photosensitive oxalid paper (Azon Corporation, Dallas, TX, USA). Metres were constructed from 35 mm plastic

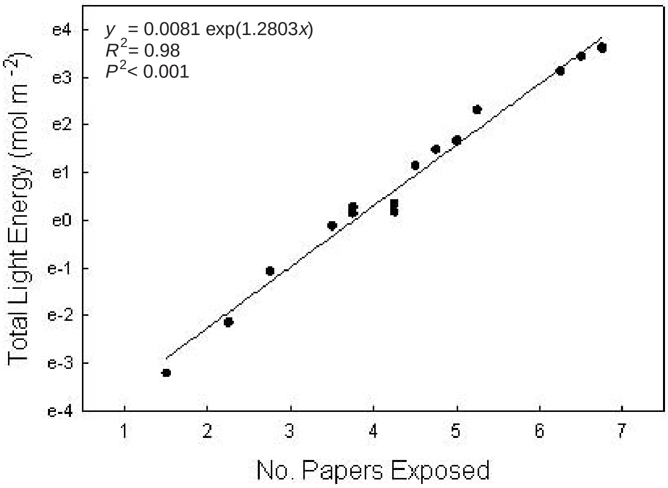

Figure 1. Relationship between the integrated light energy (PAR_{int}) in mol m^{-2} and the number of papers exposed (N), as results from the calibration of the diazo papers.

bacterial plating dishes. We attached velcro closures to the bottom of the dishes, and to the tops of plastic clothespins, allowing for easy darkroom assembly. The clothespins can be used to attach the metres to metal stakes varying in height, or to specific areas of a focal seedling. Stacks of ten 1 cm-square diazo sheets were used for exposure times of 24 hours. Metres were developed in the field using ammoniac vapour, from which the number of exposed sheets was estimated to the nearest eighth of an exposure, using a template.

We calibrated the papers using a sampling procedure similar to that described by Bardon et al. [2], in which a gradient of light energy was created by varying the exposure time to a relatively constant level of radiation. Calibrations were conducted on a clear day in three shadehouses of varying light intensity, using Li-Cor quantum sensors calibrated to measure photosynthetically active radiation (*PAR*), attached to a Campbell data logger (Campbell Scientific Inc., Logan, UT, USA). In each shadehouse, 30 light metres were arranged in random positions of a 5 × 6 matrix, with 20 cm in between light metres. Five quantum sensors were placed at the corners and in the centre of each matrix, reporting data every five minutes to the data logger. Every two hours from dawn (6 am) until dusk (6 pm), five replicate light metres were harvested at random from each shadehouse. In total, this resulted in 18 points which were then used to conduct regressions. Calibrations were performed with two dependent variables, the maximum instantaneous measure of *PAR* (μmol m^{-2} s^{-1}) received by any of the five quantum sensors in the shadehouse during the period the light metre was exposed, and the mean among the five quantum sensors for the total integrated light energy (mol m^{-2}) received for the period ending when the light metre was removed from the shadehouse.

The relationship between the number of papers exposed and the maximum instantaneous *PAR* received by the quantum sensors differed significantly among the three shadehouses. However, the relationship with the total integrated light energy was consistent across shadehouses and expresses as: PAR_{int} = 0.0081 exp(1.2803N) mol m^{-2} (R^2 = 0.98; see *figure 1*).

2.7. Measurement procedure

Measurements were made along three 250 m transects oriented south-north, on two plots in treatments 2 and 3, plus a control plot. Every 10 m a sampling point was set (26 points per transect) and indicated by a stake. In addition, 95 seedlings were selected within a one-hectare area in a plot in treatment 1. Conspecific seedlings of *Dicorynia guianensis* Amshoff (Caesalpiniaceae) were selected because they are spatially-aggregated, abundant, and easy to identify. Both transects and seedlings were chosen to provide the greatest heterogeneity in light conditions within a plot, independently from one plot to another. The spatial coordinates of all sampling points and sampled seedlings were recorded.

Measurements were performed twice at the same place and at the same hour on two different days. To study the spatial variations of measurements, measurements

Table I. List of the measurements that were performed. T0 indicates the transect on the control plot, T2 the transect in treatment 2, and T3 the transect in treatment 3. Seedlings are in treatment 1. ΔR: distance from stake or from seedling at which the measure is taken; H: height at which the measure is taken (H_i is the height of the seedling); *Rep.*: number of repeated measurements at the same place and at the same hour on different days; *Pts.* = number of sampling points; *Meas.*: number of measures = (number of sampling points) × (number of repetitions) × (number of ΔR + number of H – 1) – (number of unusable measures).

Instrument	Location	ΔR (cm)	H (m)	*Rep.*	*Pts.*	*Meas.*
LAI-2000 PCA	T0, T3	0	1.30	1	52	46
LAIL	T0, T2, T3	0	1.30	1	78	71
	seedlings	0 to 50 by 10	H_i, H_i + 0.2, H_i + 0.5, H_i + 1	2	95	1404
Densiometre	T0, T3	0	1	1	52	47
	T2	0	1	2	26	48
	seedlings	0, 50	1	1	95	190
Hemispherical photographs	T0, T2, T3	0	1.30	1	78	210
	seedlings	0, 50, 100	H_i, H_i + 0.7	1	95	214
Photosensitive paper	T0, T2, T3	0	0.40	1	78	71
	seedlings	10	0.40	1	95	95

were also performed at the sampling point, at a distance ΔR from it in a random direction, and at a distance ΔH above it.

Two LAI-2000 PCA were used, installed on a tripod at a height of 1.30 m and orientated to the north. One recorded automatically every 30 seconds the above-canopy diffuse sky radiation, from the south extremity of a 0.7 ha clearing. A view cap restricted the view of the sensor to an azimuthal 90° sector. The other LAI-2000 PCA was brought at the sampling points to measure the below-canopy diffuse sky radiation. Each measure was the average of four records at the extremities of four 50 cm long, orthogonal cross branches at a height of 1.30 m. Data were collected early in the morning (7:00–8:30) or late in the afternoon (16:45–17:45), when the solar elevation was low, to get diffuse radiation only.

A measurement with the LAIL consisted of the average of three measures taken over an interval of 30 seconds. The operator remained beneath the instrument. Data were collected between 11:00 and 14:30.

Hemispherical photographs were taken at the same schedule as the LAI-2000 PCA to avoid direct radiation. The camera was oriented so that the top of each photograph pointed north in order to calculate suntracks for analysis.

Diazo paper metres were attached to metal stakes at a height of 40 cm. When a seedling was sampled, the stake was installed 10 cm to the north.

Data were collected from April to May 1999. However, some instruments were only available for a shorter period, and it was not possible to perform measurements with all instruments at all sampling points, and to measure spatial and temporal variation for each instrument. *Table I* summarizes the measurements that were completed.

2.8. Collected variables

The instruments give four kinds of "light" variables: (1) the plant area index (*PAI*) is measured by the LAI-2000 PCA, hemispherical photographs, and the LAIL; (2) the sky openness, which is the percentage of sky which is not blocked by plant elements after projection on an hemisphere, is measured by hemispherical photographs and the densiometre; (3) the diffuse non-interceptance (*DIFN*), which is the amount of diffuse light passing through the overstorey canopy, expressed as a fraction of open-sky diffuse light, is estimated by the LAI-2000 PCA; (4) diazo papers give an estimate of the integrated photosynthetically active radiation over a daytime exposure (PAR_{int}).

The calculations of *PAI* and *DIFN* by the LAI-2000 PCA were performed after removal of none, one, or two outermost rings, thus providing three estimates of each variable. Similarly, the computations of *PAI* and sky openness from hemispherical photographs were performed after restriction to the same three zenithal ranges than those used with the LAI-2000 PCA. We thus obtained a total of 15 light variables.

From the data collected on the Paracou permanent plots, some distance-dependent stand variables were also calculated, including the number N_D of trees whose diameter is greater than D within a radius of 10 m from the sampling point (D = 10 to 70 by 10 cm), as well as their cumulated basal area B_D. These indices were computed from the latest available inventory, dating from 1997. A qualitative stand variable, denoted DAM, was also collected for seedlings only. It describes the damages caused by treatment 1 in 1987, according to five levels denoted DAM1 to DAM5: DAM1 is untouched understorey, that is to say a spot that was not affected by the 1987 logging; DAM2 corresponds to skid trails; DAM3 corresponds to treefall gaps dating from the 1987 logging; DAM4 corresponds to more recent treefall gaps (there is actually only one recent gap in the inventoried zone, which was created in 1997); DAM5 corresponds to a 1.50 m wide walking trail.

2.9. Data analysis

Spatial autocorrelation analysis was first performed on the light variables on transects, to test whether they could be considered as independent variables or whether a spatial pattern occured.

To assess the consistency between light variables, we performed correlation analysis rather than comparison of samples, because we had light variables of different kinds (PAI, PAR_{int}, sky openness, etc.) without any direct estimates of these variables that could stand as references [32]. Correlation analysis relies on relative variations; some studies that compare direct (or semi-direct) and indirect estimates [6, 9, 16, 18, 23, 35, 50] have shown precisely that the indirect methods often lead to a bias, yet are able to assess temporal and spatial relative variations.

The relationship between a variable measured at the sampling point and the same variable measured with a small spatial displacement, everything being equal in other respects, was quantified by Pearson's correlation coefficient. The self-consistency of the two measurements was tested by a Wilcoxon signed rank test for paired data. The self-consistency of light variables when measured at the same time on different days was analysed in the same way.

The relationship between light variables and quantitative stand variables (N_D and B_D) was tested with Pearson's correlation coefficient, whereas an analysis of variance was used to test the relationship between light variables and the qualitative stand variable DAM. An ANOVA was also used to test for differences among plots receiving different treatments.

3. RESULTS

3.1. Consistency of light variables

No significant (at the 5% level) spatial autocorrelation appeared on transects, for any light variable. The observations may thus be considered as independent. Two groups of variables could be discriminated: "foliage" variables (such as PAI), that increase when foliage density increases; "openness" variables (such as PAR_{int}, $DIFN$, sky openness, densiometre) that decrease when foliage density increases.

Figure 2 shows the distribution of each variable on transects. The sky openness estimated by the densiometre was significantly more than the sky openness estimated from hemispherical photographs (Wilcoxon signed rank test for paired data: p-value < 0.006 in all three cases). The estimates of PAI according to the LAI-2000 PCA, to the LAIL and to hemispherical photographs also differed significantly (Wilcoxon signed rank test for paired data: p-value < 0.006) except for one of the 15 possible comparisons, namely EPAI as compared to PAI_1 (see *figure 2*; p-value = 0.57).

Scatterplots between all 15 light variables did not visually reveal any marked nonlinear relationship, except PAR_{int} that presented an exponential relationship with the other variables. A logarithm transform was thus applied to PAR_{int} prior to any analysis. The variables were approximately normally distributed. *Table II* shows Pearson's correlation matrix between all 15 variables on transect. *Table III* shows the correlation matrix for the data on seedlings. Correlation coefficients between variables that are issued from the same instrument must be of course disregarded. The sign of the coefficient discriminated "openness" variables from "foliage" variables.

Table II revealed consistency between the diazo papers (PAR_{int}), the LAI-2000 PCA ($DIFN$ or PAI), and the LAIL. Pearson's coefficients (denoted ρ) between these variables were all significant at the 5% level, and ranged in absolute value from 0.34 to 0.64. For the LAI-2000

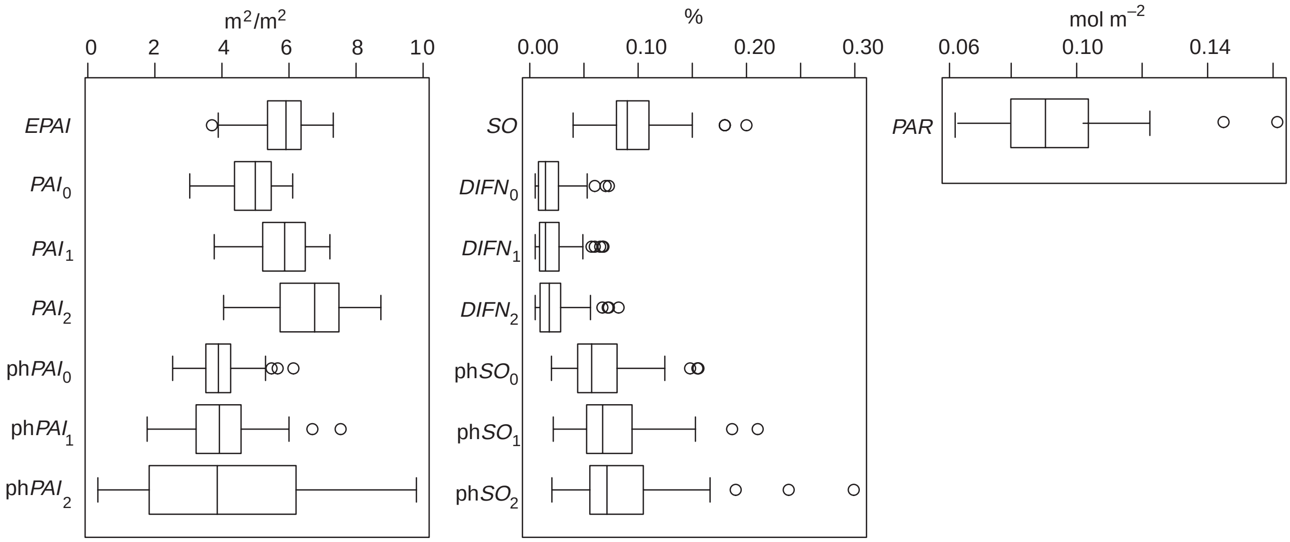

Figure 2. Boxplots of the light variables on transects. Right: "openness" variables (*SO*: sky openness estimated by the densiometre; *PAR*: PAR_{int} estimated by diazo papers; $DIFN_i$, $i = 0, 1, 2$: estimate of *DIFN* by the LAI-2000 *PCA* when disregarding *i* outermost zenithal rings; phSO_i, $i = 0, 1, 2$: estimate of the sky openness by hemispherical photographs when disregarding *i* outermost zenithal rings); left: "foliage" variables (*EPAI*: estimate of *PAI* by the LAIL; PAI_i, $i = 0, 1, 2$: estimate of *PAI* by the LAI-2000 *PCA* when disregarding *i* outermost zenithal rings; phPAI_i, $i = 0, 1, 2$: estimate of *PAI* by hemispherical photographs when disregarding *i* outermost zenithal rings).

PCA, the best correlations with PAR_{int} or with the *PAI* estimates from the LAIL were obtained when one outermost ring was disregarded.

On the contrary, the densiometre gave data on the transects that were hardly consistent with the other instruments: the sky openness estimated by the densiometre was significantly correlated (at the 5% level) only with the LAIL ($\rho = -0.34$) and with the sky openness estimated from hemispherical photographs with the narrowest zenithal range ($\rho = 0.29$).

No significant correlation except one (see *table II*) was obtained between the *PAI* estimated from hemispherical photographs and the other instruments. However, consistent significant correlations were obtained between the sky openness estimated from hemispherical photographs and the data from diazo papers, from the LAI-2000 PCA, or from the LAIL ($0.32 \leq |\rho| \leq 0.56$). The best correlations were also obtained when one outermost ring is disregarded.

Similar results were obtained from seedling data (*table III*). However, the densiometre performed better here: significant correlations were obtained with PAR_{int}, the sky openness estimated from hemispherical photographs, and the *PAI* estimated by the LAIL ($0.41 \leq |\rho| \leq 0.68$).

3.2. Spatial and temporal variability

Only the LAIL and the densiometre were used twice in the same conditions, on two different days. Pearson's correlation coefficient between the two measurements equalled 0.373 for the LAIL and 0.70 for the densiometre (both significant at the 1% level). The Wilcoxon signed rank test did not reveal any difference between the two measurements at the 5% level.

Three instruments were used twice with a small spatial displacement, either horizontally or vertically, on seedlings (*table I*). The LAIL was tested against a horizontal displacement of 10 to 50 cm (with a 10 cm step): Pearson's correlation coefficient between the original measure and the displaced one ranged from 0.79 to 0.85 (always significant at the 5% level), and the Wilcoxon signed rank test did not reveal any difference between the two measurements at the 5% level.

It was also tested against a vertical displacement of 20, 50 or 100 cm: in all three cases the correlation coefficient was significantly different from zero ($\rho > 0.82$) but the Wilcoxon test indicated that the *PAI* measure at height *H* was significantly greater on average than its measure at height *H* + 20, + 50, or + 100 cm (*p*-value < 0.003). It also showed that the *PAI* measure at height

Table II. Pearson's correlation matrix between the 15 light variables on transects. The first 8 variables are "openness" variables, whereas the remaining 7 variables are "foliage" variables. Shaded areas indicate the couples of variables that are issued from a common device (and should not be taken into account). * indicates significance at the 5% level, ** at the 1‰ level. *SO*: sky openness estimated by the densiometre; *PAR*: ln(PAR_{int}) estimated by diazo papers; $DIFN_i$, i = 0, 1 ,2: estimate of *DIFN* by the LAI-2000 PCA when disregarding *i* outermost zenithal rings; phSO_i, i = 0, 1, 2: estimate of the sky openness by hemispherical photographs when disregarding *i* outermost zenithal rings; *EPAI*: estimate of *PAI* by the LAIL; PAI_i, i = 0, 1, 2: estimate of *PAI* by the LAI-2000 PCA when disregarding *i* outermost zenithal rings; phPAI_i, i = 0, 1, 2: estimate of *PAI* by hemispherical photographs when disregarding *i* outermost zenithal rings.

	SO	*PAR*	$DIFN_0$	$DIFN_1$	$DIFN_2$	phSO_0	phSO_1	phSO_2	EPAI	PAI_0	PAI_1	PAI_2	phPAI_0	phPAI_1	phPAI_2
SO	1	0.15	0.134	0.102	0.081	0.121	0.196	0.290*	–0.337**	–0.067	–0.023	–0.129	0.016	0.164	0.185
PAR		1	0.445**	0.492**	0.363*	0.458**	0.487**	0.524**	–0.450**	–0.412**	–0.406**	–0.342*	–0.150	0.093	0.178
$DIFN_0$			1	0.989**	0.920**	0.490**	0.508**	0.441**	–0.643**	–0.876**	–0.851**	–0.749**	–0.183	–0.062	0.080
$DIFN_1$				1	0.902**	0.509**	0.524**	0.461**	–0.639**	–0.862**	–0.856**	–0.731**	–0.199	–0.057	0.101
$DIFN_2$					1	0.411**	0.410**	0.316*	–0.530**	–0.769**	–0.759**	–0.765**	–0.131	–0.094	0.028
phSO_0						1	0.955**	0.854**	–0.349**	–0.561**	–0.541**	–0.475**	–0.700**	–0.317**	–0.068
phSO_1							1	0.945**	–0.406**	–0.553**	–0.529**	–0.513**	–0.588**	–0.237*	–0.013
phSO_2								1	–0.458**	–0.509**	–0.462**	–0.498**	–0.422**	–0.029	0.093
EPAI									1	0.580**	0.592**	0.407**	0.009	–0.161	–0.253*
PAI_0										1	0.961**	0.855**	0.247	0.036	–0.052
PAI_1											1	0.800**	0.209	0.051	–0.045
PAI_2												1	0.165	0.055	0.023
phPAI_0													1	0.629**	0.311**
phPAI_1														1	0.779**
phPAI_2															1

Table III. Pearson's correlation matrix between the 9 light variables on seedlings. The first 5 variables are "openness" variables, whereas the remaining 4 variables are "foliage" variables. Shaded areas indicate the couples of variables that are issued from a common device (and should not be taken into account). * indicates significance at the 5% level, ** at the 1‰ level. *SO*: sky openness estimated by the densiometre; *PAR*: ln(PAR_{int}) estimated by diazo papers; phSO_i, i = 0, 1, 2: estimate of the sky openness by hemispherical photographs when disregarding *i* outermost zenithal rings; *EPAI*: estimate of *PAI* by the LAIL; phPAI_i, i = 0, 1, 2: estimate of *PAI* by hemispherical photographs when disregarding *i* outermost zenithal rings.

	SO	*PAR*	phSO_0	phSO_1	phSO_2	*EPAI*	phPAI_0	phPAI_1	phPAI_2
SO	1	0.606**	0.681**	0.603**	0.406**	–0.533**	0.203	0.15	–0.068
PAR		1	0.672**	0.534**	0.339**	–0.478**	0.084	0.077	–0.156
phSO_0			1	0.858**	0.464**	–0.536**	0.037	0.123	–0.203
phSO_1				1	0.815**	–0.559**	–0.115	–0.077	–0.256*
phSO_2					1	–0.437**	–0.204	–0.128	–0.17
EPAI						1	–0.24*	0.005	0.22*
phPAI_0							1	0.448**	0.008
phPAI_1								1	0.472**
phPAI_2									1

$H + 20$ cm was significantly greater on average than the measure at $H + 50$ cm (p-value = 0.003), whereas the measure at $H + 50$ was not significantly different from that at $H + 100$ cm (p-value = 0.678).

The densiometre was tested against a horizontal displacement of 50 cm. Pearson's correlation coefficient equalled 0.85 (significantly different from 0 at the 5% level) but the Wilcoxon test indicated that the two measures had different distributions (p-value = 0.009).

Finally, hemispherical photographs were tested against a horizontal displacement of 50 and 100 cm: Pearson's correlation coefficient between the original measure and the displaced one ranged from 0.57 to 0.82, depending on the number of disregarded zenithal rings (always significant at the 5% level), and the Wilcoxon signed rank test did not reveal any difference between the two measurements at the 5% level.

Hemispherical photographs were also tested against a vertical displacement of 70 cm: whatever the number of disregarded zenithal rings, the correlation coefficient was significantly different from zero ($\rho > 0.78$), but the Wilcoxon test indicated that the sky openness measure at height H was significantly less on average than its measure at $H + 70$ cm (p-value < 0.042).

3.3. Relationship between light and stand variables

Table IV shows Pearson's correlation coefficient between light and stand variables. The data from the LAI-2000 PCA (*PAI* or *DIFN*) were significantly (at the 5% level) correlated with most of the stand structure variables N_D or B_D, for D ranging from 10 to 70 cm. Pearson's correlation coefficients however were low ($0.29 \leq |\rho| \leq 0.44$ for *PAI*, $0.29 \leq |\rho| \leq 0.36$ for *DIFN*). The best correlations were obtained when no outermost zenithal ring was disregarded before the computation of *PAI* and *DIFN* (variables denoted PAI_0 and $DIFN_0$ in *table IV*). Also better correlations were obtained with the number of trees N_D than with the basal area B_D.

A few significant correlations were also obtained between the data from hemispherical photographs (*PAI* or sky openness) and N_D or B_D ($0.23 \leq |\rho| \leq 0.27$). Actually eight coefficients, out of a 14×6 matrix of correlations, were significant at the 5% level, and the number of disregarded zenithal rings prior to the calculation of *PAI* and sky openness did not influence the quality of the correlations. As for the other instruments (LAIL, densiometre, diazo papers), only one significant correlation was obtained with stand structure variables.

Surprisingly, the sign of the significant correlations, ρ, was negative for the light variables that increase with foliage density ("foliage" variables), and positive for the light variables that decrease with foliage density ("openness" variables). As N_D and B_D are strongly correlated in a positive way, this suggested that the greater the number of trees or basal area was, the greater the amount of incident light. Because the mean density of trees and the mean basal area decrease from control plots to treatment 3, we also examined light variables within and among transects.

When calculating the correlation coefficients separately for each transect, most correlations (594 out of 630) turned to be non-significant at the 5% level. Thus, the significant correlations that were obtained with the LAI-2000 PCA and hemispherical photographs mostly reflected the contrasts between transects rather than the within-transect variability. For example, differences among transects for the sky openness estimated from hemispherical photographs are illustrated in *figure 3*. The frequency distribution of the variable differed markedly among transects; moreover, the variance decreased as the intensity of the logging treatment increased (one-sided F-test to compare the variance on T0 et T2: p-value = 0.057; on T2 and T3: p-value = 0.008; on T0 and T3: p-value < 0.001).

An analysis of variance for transect-level differences is presented in *table V*. It shows that, apart from the densiometre, all instruments were able to discriminate between the two transects that have received extreme logging treatments (treatment 3 versus control), but that no instrument was able to distinguish between transects with treatments 2 and 3 (the test however was not conducted with the LAI-2000 PCA since it was not used on transect T2, see *table I*). *Table V* also suggested a positive relationship between logging intensity and *PAI*, and a negative relationship between logging intensity and the sky openness, *DIFN* and PAR_{int}.

Table VI shows the analysis of variance of light variables with respect to the qualitative stand variable DAM for seedlings. It shows that all instruments used (the LAI-2000 PCA was not used for seedlings) discriminated the recent treefall gap from the other sites. The LAIL and diazo papers did not make any distinction within the other sites, whereas the densiometre distinguished the trail from understorey, and hemispherical photographs distinguished the former logging track from understorey. As expected, the *PAI* was lowest in the recent gap and increased till understorey, whereas sky openness and PAR_{int} were highest in the recent gap and decreased till understorey.

Table IV. Pearson's correlation matrix between the 15 light variables and the 14 stand variables on transects. Shaded areas indicate the couples of variables that are issued from a common device (and should not be taken into account). * indicates significance at the 5% level, ** at the 1‰ level. *SO*: sky openness estimated by the densiometre; *PAR*: $\ln(PAR_{int})$ estimated by diazo papers; $DIFN_i$, $i = 0, 1, 2$: estimate of *DIFN* by the LAI-2000 PCA when disregarding *i* outermost zenithal rings; phSO_i, $i = 0, 1, 2$: estimate of the sky openness by hemispherical photographs when disregarding *i* outermost zenithal rings; *EPAI*: estimate of *PAI* by the LAIL; PAI_i, $i = 0, 1, 2$: estimate of *PAI* by the LAI-2000 PCA when disregarding *i* outermost zenithal rings; phPAI_i, $i = 0, 1, 2$: estimate of *PAI* by hemispherical photographs when disregarding *i* outermost zenithal rings; N_D, B_D: number of trees, and their cumulated basal area, whose diameter is greater than *D* (in cm) within 10 m.

	SO	*PAR*	$DIFN_0$	$DIFN_1$	$DIFN_2$	phSO_0	phSO_1	phSO_2	*EPAI*	PAI_0	PAI_1	PAI_2	phPAI_0	phPAI_1	phPAI_2
N_{10}	–0.224	0.009	0.203	0.225	0.242	0.270*	0.197	0.113	0.222	–0.162	–0.194	–0.286	–0.247*	–0.221	–0.199
N_{20}	–0.166	0.046	0.347*	0.348*	0.247	0.145	0.077	0.011	0.086	–0.400**	–0.403**	–0.313*	–0.162	–0.185	–0.219
N_{30}	–0.229	–0.161	0.176	0.179	0.180	–0.006	–0.059	–0.102	0.146	–0.214	–0.249	–0.185	–0.006	–0.099	–0.233*
N_{40}	–0.361**	0.094	0.326*	0.333*	0.280	0.005	0.019	0.010	–0.005	–0.440**	–0.428**	–0.347*	0.143	0.134	–0.033
N_{50}	–0.122	0.167	0.300*	0.300*	0.295*	0.098	0.109	0.131	–0.107	–0.342*	–0.329*	–0.283	0.015	0.031	–0.129
N_{60}	–0.122	0.112	0.370*	0.358*	0.313*	0.191	0.202	0.192	–0.201	–0.406**	–0.366*	–0.272	–0.050	–0.032	–0.138
N_{70}	–0.061	0.198	0.312*	0.297*	0.244	0.181	0.242*	0.227	–0.030	–0.291*	–0.214	–0.143	–0.034	–0.011	–0.082
B_{10}	–0.200	0.081	0.337*	0.340*	0.316*	0.188	0.184	0.151	0.064	–0.361*	–0.332*	–0.273	–0.060	–0.054	–0.182
B_{20}	–0.183	0.085	0.345*	0.346*	0.305*	0.164	0.167	0.143	0.031	–0.383**	–0.348*	–0.267	–0.034	–0.031	–0.165
B_{30}	–0.206	0.036	0.294*	0.297*	0.277	0.129	0.138	0.122	0.040	–0.327*	–0.302*	–0.223	0.003	–0.005	–0.159
B_{40}	–0.216	0.154	0.304*	0.308*	0.276	0.141	0.183	0.184	–0.043	–0.344*	–0.297*	–0.218	0.045	0.080	–0.055
B_{50}	–0.101	0.180	0.272	0.275	0.264	0.180	0.218	0.232*	–0.076	–0.280	–0.234	–0.177	–0.017	0.026	–0.098
B_{60}	–0.096	0.144	0.294*	0.292*	0.260	0.220	0.256*	0.255*	–0.113	–0.299*	–0.238	–0.159	–0.048	–0.003	–0.099
B_{70}	–0.035	0.160	0.178	0.181	0.158	0.171	0.231	0.236*	0.024	–0.150	–0.080	–0.033	–0.020	0.026	–0.039

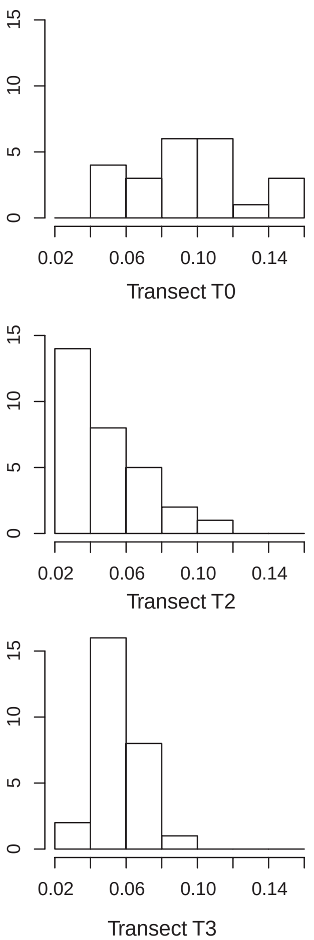

Figure 3. Histogram of the light variable phSO_1 (phSO_1: sky openness estimated from hemispherical photographs when disregarding one outermost zenithal ring) on the three transects: T0 is the transect on the control plot, T2 is the transect in treatment 2, and T3 is the transect in treatment 3.

Table V. Analysis of variance of light variables with respect to transects. PAI_0: estimate of *PAI* by the LAI-2000 PCA without disregarding any zenithal ring; $DIFN_0$: estimate of *DIFN* by the LAI-2000 PCA without disregarding any zenithal ring; *EPAI*: estimate of *PAI* by the LAIL; *SO*: sky openness estimated by the densiometre; phSO_1: estimate of the sky openness by hemispherical photographs when disregarding one outermost zenithal ring; *PAR*: ln(PAR_{int}) estimated by diazo papers.

Variable	Transect	Mean[a]	*F* statistic[b]
PAI_0	T0	4.51 (A)	39.3 **
	T3	5.44 (B)	(*df*: 1, 44)
$DIFN_0$	T0	0.028 (A)	21.7 **
	T3	0.011 (B)	(*df*: 1, 44)
EPAI	T0	5.60 (A)	3.62 *
	T2	5.77 (AB)	(*df*: 2, 67)
	T3	6.19 (B)	
SO	T0	0.090 (A)	0.87
	T2	0.094 (A)	(*df*: 2, 68)
	T3	0.102 (A)	
PAR	T0	–2.301 (A)	4.74 *
	T2	–2.454 (B)	(*df*: 2, 69)
	T3	–2.467 (B)	
phSO_1	T0	0.111 (A)	24.4 **
	T2	0.058 (B)	(*df*: 2, 67)
	T3	0.063 (B)	

[a] Two means that are followed by a common letter are not significantly different at the 5% level according to a Ryan-Einot-Gabriel-Welsch multiple-range test (procedure ANOVA of SAS, SAS Institute Inc., Cary, NC, USA).
[b] * indicates significance at the 5% level; ** indicates significance at the 1‰ level.

4. DISCUSSION AND CONCLUSIONS

The LAI-200 PCA, the LAIL and diazo papers offered consistent information on the light environment in the understorey. Hemispherical photographs also provided consistent estimate of sky openness, but failed to provide consistent estimates of *PAI* (*tables II* and *III*). This failure, which contrasts with other studies [9, 35], may have resulted from the selection of the threshold value needed to distinguish black from white pixels on the digitized images, or from an inadequate algorithm for averaging light transmittances [6, 18, 35, 50]. The densiometre also exhibited little success, here as in other studies [17]: Its data are weakly correlated with those of the other instruments.

The correlation coefficients however remained low, which can be explained by the understorey situation and by the weak range of variation that results from it [17]: The “openness” variables varied up to 15-fold, whereas the *PAI* estimates (excluding the estimate from hemispherical photographs) did not vary up more than 2-fold on transects (*figure 2*). Still the *PAI* estimates (between 3 and 9) are comparable to those obtained in other forests [14, 16, 35, 46].

Table VI. Analysis of variance of light variables with respect to the DAM variable on seedlings. *EPAI*: estimate of *PAI* by the LAIL; *SO*: sky openness estimated by the densiometre; phSO_1: estimate of the sky openness by hemispherical photographs when disregarding one outermost zenithal ring; *PAR*: ln(PAR_{int}) estimated by diazo papers.

Variable	DAM[a]	Mean[b]	*F* statistic[c]
EPAI	DAM4	4.65 (A)	13.37 **
	DAM3	5.74 (B)	(*df*: 4, 81)
	DAM5	5.98 (B)	
	DAM2	6.40 (B)	
	DAM1	6.49 (B)	
SO	DAM4	0.158 (A)	15.11 **
	DAM5	0.118 (B)	(*df*: 4, 79)
	DAM3	0.093 (BC)	
	DAM2	0.089 (BC)	
	DAM1	0.084 (C)	
PAR	DAM4	–2.121 (A)	10.33 **
	DAM3	–2.361 (B)	(*df*: 4, 89)
	DAM5	–2.410 (B)	
	DAM1	–2.469 (B)	
	DAM2	–2.540 (B)	
phSO_1	DAM4	0.128 (A)	25.57 **
	DAM2	0.074 (B)	(*df*: 4, 72)
	DAM3	0.068 (BC)	
	DAM5	0.053 (BC)	
	DAM1	0.049 (C)	

[a] DAM1: understorey; DAM2: logging track; DAM3: former treefall gap; DAM4: recent treefall gap; DAM5: trail.
[b] Two means that are followed by a common letter are not significantly different at the 5% level according to a Ryan-Einot-Gabriel-Welsch multiple-range test (procedure ANOVA of SAS).
[c] ** indicates significance at the 1‰ level.

Not surprisingly then, the instruments succeeded in discriminating contrasted situations, but were less successful in discriminating intermediary situations. At the local scale, all instruments distinguished gap versus understorey, but they were not able to discriminate between logging track, former treefall gap and trail (*table VI*). At the plot scale, the silvicultural treatments generate contrasts that were detected by all instruments except the densiometre. As transects were chosen so as to maximise the intra-plot variability without influencing the inter-plot variability, silvicultural treatments are harder to detect than they would be with a completely random sampling design. Our results suggest that 12 years after logging, more intense logging activity results in a higher variance of light variables (*figure 3*). This result is in agreement with Nicotra et al. [32] and indicates that the entire distribution of light variables should be examined and not simply their mean level.

The negative correlation that we found between *PAI* and the basal area (or similarly the positive correlation between sky openness and the basal area) may be surprising. In fact the logged plots that we studied have been invaded by lianas and saplings that contribute heavily to the LAI although their basal area is not taken into account in our inventories. Thus, light availability may decrease in logged plots due to shading from stems less than 10 cm DBH. For example, sky openness in the control plot (11%), as estimated by hemispherical photographs, is almost twice that observed in logged plots (6%) (*table V*). In a somewhat similar way, Planchais and Pontailler [35] measured a higher LAI in a young beech stand than in an old one.

Stand structure variables, commonly used in models of forest dynamics to reflect competition processes for light and nutrients through two-sided competition indices, or specifically for light through one-sided competition indices, have proven useful in explaining the growth of trees more than 10 cm DBH at Paracou [20, 21]. However, in the present study, no significant relationship could be obtained between light variables and the simplest of those indices (number of trees and basal area within 10 m). This result contrasts with Comeau et al. [12] who detected significant relationships between light variables and Lorimer's competition index, in a mixed birch stand where they measured the diameter of *all* trees. One explanation of our result which is consistent with that of Comeau et al. [12] is that the light environment is sensitive to the density and structure of the vegetation below 10 cm DBH. Unfortunately, this also implies that classical data on the overstorey will not be accurate enough to model the understorey dynamics of light and its potential influence on regeneration.

The spatial sensitivity of measurements was investigated with small displacements, for three instruments (*table I*). When the displacement is horizontal (distances up to 1 m), the correlation coefficients are elevated (about 0.8) and the Wilcoxon does not reveal any significant difference of the mean, which simply signifies that the two measures are similar at each point. The spatial dependence probably goes over 1 m but it stops before 10 m, as the spatial autocorrelation analysis on transects did not detect any dependence.

Results in the literature on the spatial dependence of light measurements are contrasted: Baraloto and Couteron (in prep.) observed spatial independence at distances as small as 50 cm for both the LAIL and the diazo paper; on the contrary Nicotra et al. [32] detected spatial dependence as far as 20 m in old-growth stands and 10 m in second-growth stands in Costa Rica. The viewing angle of the instrument, light heterogeneities such as sun flecks [7] that can be more or less minimized by the measurement procedure, can explain these differences.

When the displacement is vertical (up to 1 m), the correlation coefficients are still elevated (about 0.8) but the Wilcoxon revealed a significant difference of the mean, which signifies that the two measures varied in the same way with a systematic bias of one with respect to the other. Quite logically, the *PAI* estimate decreases and the sky openness estimate increases as the measurement height increases. A significant bias was detected with hemispherical photographs with a height difference of 70 cm, which has to be confronted to Whitmore et al. [50] who detected no difference with hemispherical photographs for height differences up to 50 cm.

According to our results, light measurements are more sensitive to a vertical displacement than to an horizontal displacement, the displacement resulting in a systematic bias. This could further be investigated theoretically by reconstructing the light environment from the canopy architecture [4, 10, 26, 40, 47].

As for time, no difference according to the Wilcoxon test could be detected between two measures repeated at a few days interval. The correlation coefficients between the two measurements were, however, quite small (smaller than for the spatial displacements), which reflects large amount of temporal variability [44]. On a yearly basis in a tropical forest in Panama, Smith et al. [41] recorded even greater changes using hemispherical photographs.

Eventually, the LAI-2000 PCA and hemispherical photographs certainly provide the most consistent information in the understorey. As an alternative to these expensive and cumbersome instruments, the LAIL and diazo papers offer a quick and simple way to characterize the light environment in understorey. The empirical LAI-metre, although attractive by its price (about $50), still has to prove that it is a valuable instrument and that its empirical component (correction factor *C*) is not a serious drawback. Finally, the densiometer does not seem accurate enough in understorey [17]; its use should be limited to rapid and coarse assessments of contrasted situations [34, 48].

Acknowledgments: Funding to support this research was provided by the "XI^{e} Contrat de plan État Région Guyane". We thank S. Jésel, P. Petronelli, and Tanguy for field assistance. J.-M. Walter (Strasbourg University, France), M.-A. Dubois (CEA Saclay, France), J.-M. Guehl (INRA Nancy, France), P. Imbert (INRA Kourou, French Guyana) and D. Lo Seen (CIRAD Montpellier, France) provided technical suggestions. We also thank three anonymous reviewers who contributed to improve an earlier version of the manuscript.

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