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A calibration method for the crown illumination index for assessing forest light environments

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Abstract

The crown illumination index (CII) is an ordinal scale frequently used to qualitatively assess the light environment within a forest. Although this method provides a simple and rapid approach, it can be subjective and needs to be calibrated against quantitative measurements of canopy structure. A study was undertaken in north-western Amazonia to provide a means to calibrate the CII in tropical forests. Hemispherical photographs were taken to represent each CII class, which were then analysed using HemiView 2.1 software in order to calculate light availability factors. The proportion of visible sky and indirect, direct and global site factors (the proportion of indirect, direct and total radiation reaching a point, compared to an open location) were all found to correlate strongly with CII class and therefore offer a viable method for calibration. CII classes could only be weakly defined with respect to leaf area index (LAI), however, and so conversion of CII to LAI or vice versa is problematic. The results of this study provide a quantified description of each index class, significantly improving interpretation of the crown illumination index.

Keywords: Light availability; Crown illumination index; Hemispherical photography; Leaf area index (LAI); Amazonian forests

1. Introduction

The study of light environments within forest ecosystems is an integral part of understanding tree life history dynamics. Light is essential for photosynthesis and other plant processes, and consequently plays an important role in driving growth (e.g. Wright et al., 1998; Singhakumara et al., 2003; King et al., 2005), mortality patterns (e.g. Clark and Clark, 1992; Walters and Reich, 1996; Kobe, 1999), as well as the distribution of species (e.g. Clark and Clark, 1992; Clark et al., 1993; Davies et al., 1998). Light availability varies considerably within multi-layered forest canopies, and therefore with each tree's position in this vertical profile. Also, there are marked horizontal variations in light availability; within tropical forests often only 1–2% of full sunlight penetrates to the understorey, while 20–35% of full sunlight reaches the ground layer at the centre of large canopy gaps (Chazdon and Fetcher, 1984). Therefore the ability to characterise light environments is important for understanding forest dynamics and studying plant adaptations to varying light conditions.

It is possible to directly measure light availability in terms of photosynthetically active radiation (PAR) or photosynthetic photon flux density (PPFD). However, these methods require specialist equipment (e.g. pyranometers, quantum sensors) as well as access to the forest canopy, which is usually problematic. Also, unless these measurements can be repeated over a period of time such methods provide only an instantaneous view of the light environment. Alternatively, indirect methods that categorise the light environment based on an ordinal scale provide a simpler and more rapid approach and are often better suited to providing an estimate of light environment integrated over a longer period. Dawkins and Field (1978) devised the "crown position index" to describe a tree's light environment based on a five-point scale ((1) no direct light; (2) crown lit only from side; (3) partial (10–90%) vertical illumination; (4) full vertical illumination; (5) crown fully exposed to lateral and vertical light). This scale was later adapted by Clark and Clark (1992), who found that the majority of saplings in a Costa Rican forest fell into class 2, and suggested subdividing this class into low, medium and high lateral light. Clark and Clark's modified scale (the crown illumination index, or CII, Table 1), has been widely used for assessing the light environment of individual trees

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Table 1
Crown illumination index definitions, from Clark and Clark, 1992 (adapted from Dawkins and Field, 1978)

Index value	Definition
1	No direct light (crown is not lit directly vertically or laterally)
1.5	Low lateral light
2	Medium lateral light
2.5	High lateral light
3	Some vertical light (10–90% of the vertical projection of the crown is exposed to vertical light)
4	Crown completely exposed to vertical light, lateral light blocked within some or all of the 90° inverted cone encompassing the crown.
5	Crown completely exposed to vertical and lateral light within the 90° inverted cone encompassing the crown

(e.g. Oberbauer et al., 1993; Davies and Ashton, 1999; Saenz et al., 1999; Sterck et al., 1999; Svenning, 2002; King et al., 2005; Malizia and Grau, 2006; Sheil et al., 2006; van Gelder et al., 2006). However, while the simplicity of the CII has proved attractive to ecologists, this is a generic, semi-quantitative scale, with no relation to actual quantified light measurements, and presents problems for analysis using parametric statistical methods.

Previous attempts to calibrate the crown illumination index have examined how it varies with quantitative parameters, including the percentage of open canopy (Davies et al., 1998; Poorter and Arets, 2003), the direct site factor (DSF) (Poorter and Arets, 2003), which is the proportion of direct radiation penetrating the canopy, and the global site factor (GSF) (Clark et al., 1993), the proportion of total radiation available (direct and diffuse) relative to an open site. As the site factors are site specific measures, calibrations based solely on these are not generally applicable. Also, no previous study calibrates the entire scale, with all missing the extremes or classes between 1 and 2.5 (Table 2). Moreover, only the average of each variable has been published for each CII class. The crown illumination index is not a strictly linear scale, with classes 1–2.5 narrowly differentiated, while classes 3 and 4 incorporate a broad range of light levels. Therefore reporting the range of each light variable covered by a class, as well as the average, would quantify the variation in class "width" and provide a more informative description of what each class represents.

Table 2
Previous calibrations of CII using global site factor (GSF), visible sky and direct site factor (DSF)

CII	GSF[1]	Visible sky[2]	Visible sky[3]	DSF[3]
1	–	0.029a	–	–
1.5	0.014	–	0.034i	0.059i
2	0.017	0.051b	0.034i	0.063i
2.5	0.045	–	0.034i	0.074i
3	0.104	0.074c	0.060ii	0.169ii
4		0.158d	–	–
5	–	0.355e	–	–
r_s	0.34	0.82	–	–

All are given as proportions. Statistical results from original publications. r_s is the Spearman's rank correlation coefficient. *Sources*: (1) Clark et al. (1993), la Selva, Costa Rica ($n = 424$); (2) Davies et al. (1998), Sarawak, Malaysia ($n = 101$); (3) Poorter and Arets (2003), Bolivian Amazonia ($n = 225$). (a–e) Significantly different at $P \leq 0.001$ for ANOVA on log-transformed data. (i–ii) Significantly different at $P \leq 0.05$ for Student–Newman–Keuls test.

In this paper we intend to provide a comprehensive multi-parameter calibration of the CII, including the first calibration using leaf area index, which is a widely calculated variable in forest studies. Through this calibration study we aim to improve understanding of how the CII corresponds to the light environment that plants experience and provide calibration variables which are relevant for use across the tropics.

2. Methods

We carried out the CII calibration in mature, unflooded, lowland humid tropical forest in north Peruvian Amazonia, at three sites in the Iquitos area: Allpahuayo (3°57′S, 73°26′W, 114 m), Yanamono (3°26′S, 72°51′W, 104 m) and Sucusari (3°16′S, 72°54′W, 107 m) (for regional forest and site description see Vasquez and Phillips, 2000; Malhi et al., 2002). At both Allpahuayo and Yanamono, we worked in two permanent one hectare plots. Each one hectare plot is split into subplots (Allpahuayo: 25 subplots of 20 m × 20 m, Yanamono: 10 subplots of 20 m × 50 m), sampling sites were located at the centre of 55 randomly selected subplots (Allpahuayo: $n = 37$, Yanamono: $n = 18$). At Sucusari, we used a forest canopy walkway, allowing access into the canopy up to 35 metres. This was especially valuable for providing a true representation of the light environment of emergent and canopy trees. Sampling sites were located at regular intervals along the walkway, including the towers ($n = 13$).

At each sampling site we took hemispherical photographs to obtain images representing the range of light environments encompassed within the CII scale. We used a Nikon Coolpix 5400 digital camera fitted with a fish-eye lens, mounted 1.5 metres from the ground on a tripod, with each photograph describing the light environment of a theoretical tree of that height. Photographs were taken under a uniformly overcast sky to ensure clear differentiation between the canopy and sky during analysis. Each location was assigned a CII value by one of us (HK). Sites under the forest canopy represented the light environment at the lower end of the CII scale (1–3), with larger canopy gaps providing classes 2.5 and 3. The canopy walkway represented the upper end of the scale (3 and 4).

It was important for CII classification to be undertaken consistently, as the calibration would be based upon this allocation of hemispherical photographs to index scores. Therefore we undertook a separate assessment of the "repeatability" of the CII, both between different observers and for one observer over time. To assess the potential between-observer error associated with the CII, the light environment of 54 trees within the forest at Sucusari were assessed by two independent observers (HK and one other) and the degree of concordance assessed (Kendall's tau of concordance). There is also potential for drift in a single observer's interpretation of each CII class, as well as for conditions on the day to affect decisions. The degree of wind, sun, rain and insects experienced may all potentially affect an observer's judgement of the appropriate class. Therefore, the CII of a further 111 trees at Sucusari was assessed at the beginning and end of a two week period (by HK).

The total sample size for the calibration was 68, with 13, 19, 15, 10, 7 and 4 hemispherical photographs for CII classes 1, 1.5, 2, 2.5, 3 and 4, respectively. No hemispherical photographs were taken to represent class 5 as this describes trees with both full vertical and lateral light within the 90° inverted cone encompassing the crown.

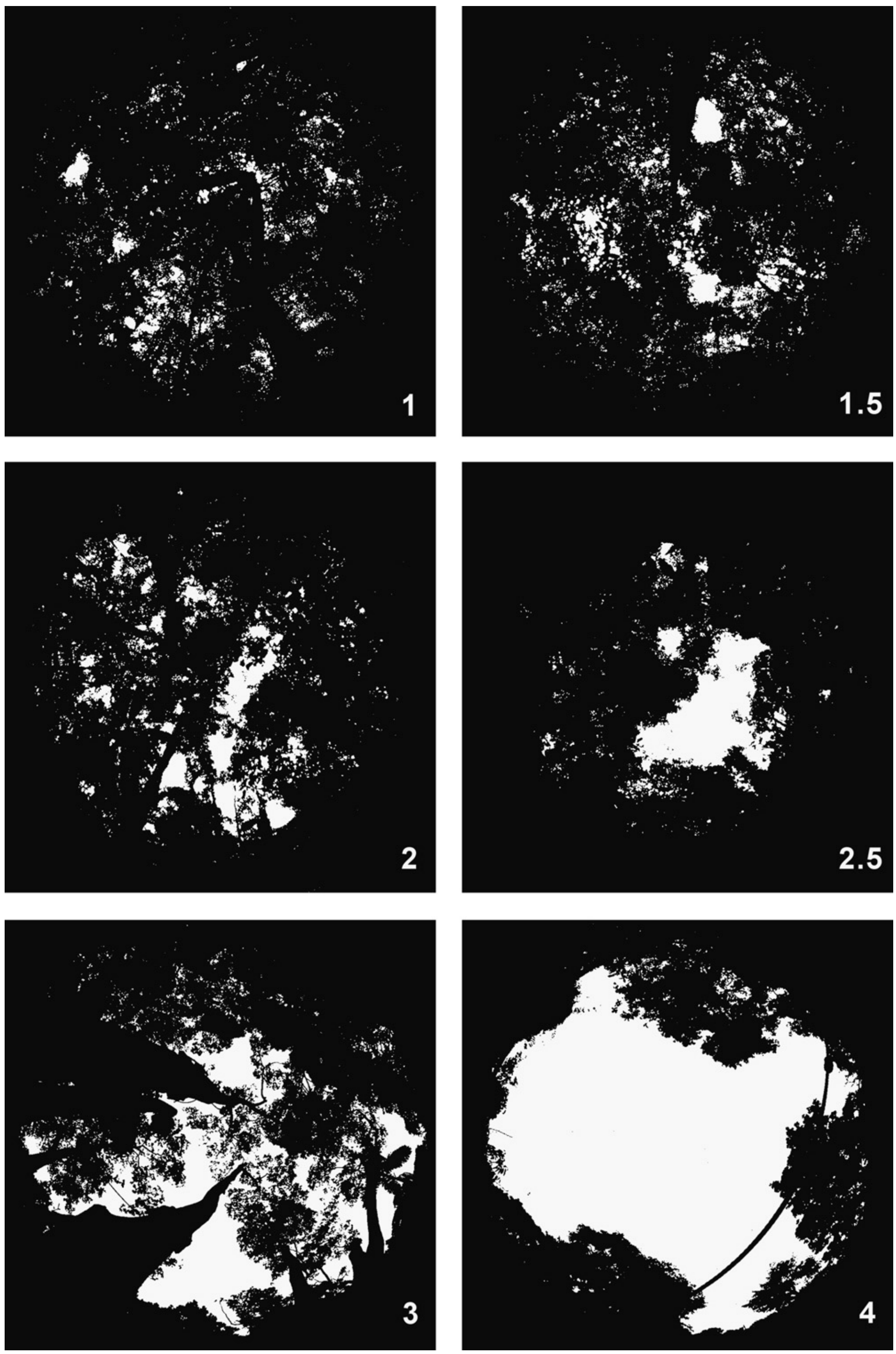

Fig. 1. Examples of hemispherical photographs representing each crown illumination index class (1–4). A threshold value is used to classify photographs as black and white images. Images classified using SideLook (M. Nobis, version 1.1: www.appleco.ch).

We analysed the hemispherical photographs using HemiView 2.1 canopy analysis software (Delta-T Devices, Burwell, Cambridge, UK). Within this program, hemispherical photographs are classified using a threshold value which applies a binary division between sky and canopy elements. This produces a black and white image, for which black represents canopy and white represents sky (Fig. 1). This image is used to calculate gap fraction and light variables for the hemisphere 0–90° from the zenith angle. The indirect, direct and global site factors were estimated for the sampling points, based on the position of canopy gaps relative to the course of sun tracks. Whereas the direct site factor describes the proportion of direct light reaching the sampling point, relative to an open location, the indirect site factor (ISF) represents the proportion of indirect or diffuse light reaching this point. The global site factor is calculated as a weighted average of the indirect and direct site factors. The ISF, DSF and GSF therefore provide useful quantitative measures of light availability, relevant to the specific latitude of each site. We also calculated the proportion of visible sky (i.e. proportion of the canopy containing gaps) which indirectly represents the potential light availability. This variable is not dependent on site-specific solar paths and is therefore invariant with location, providing a calibration for the CII that is applicable across sites.

Similarly, the leaf area index (LAI), defined as the projected one side leaf area per unit of ground area (Cutini et al., 1998), provides a non-site specific calibration for the CII. LAI was calculated for each hemispherical photograph using an inversion of Beer–Lambert's law, incorporating Miller's theorem (1967) (Leblanc et al., 2005):

$$\mathrm{LAI} = -2\int_0^{\pi/2} \frac{\ln[P(\theta)]}{\Omega(\theta)} \cos\theta \sin\theta \, \mathrm{d}\theta$$

where θ is the zenith angle, $P(\theta)$ the mean gap fraction measured at that angle (calculated using HemiView) and $\Omega(\theta)$ is a clumping index, representing the deviation of the canopy element's spatial distribution from the random case (Leblanc et al., 2005). As we lacked sufficient data to calculate site specific clumping indices, the clumping index was assumed to be 1 (i.e. randomly distributed), which is common in broadleaf forests (Leblanc et al., 2005). However, in complex tropical canopies, where the location and structure of individual trees and gaps created by disturbance mechanisms determine the distribution of "clumps" of foliage (van Gardingen et al., 1999) there may be some deviation from the random case, causing LAI values to be underestimated. Consequently, we applied ranked statistics (i.e. Spearman's correlation) to account for any systematic variation in calculated LAI.

The selection of the threshold value is a subjective process with the most appropriate classification to distinguish between sky and canopy chosen by eye. To assess whether this could substantially affect our results we undertook a checking procedure. Firstly, the threshold value for each hemispherical photograph was manually determined independently by two people, prior to generating the variable estimates with HemiView (i.e. visible sky, ISF, DSF and GSF) and calculating LAI, for each observer. A very strong correlation was found between the variables calculated using each manual threshold value (Pearson's correlation: $r = 0.978$–0.992, $P < 0.001$, $n = 68$). Secondly, we applied SideLook (M. Nobis, version 1.1: www.appleco.ch) to calculate the threshold value automatically based on edge detection, using an algorithm designed to find the highest contrast at the edges between canopy and sky (Nobis and Hunziker, 2005). There was very strong agreement between the average of variables calculated by each person using manual thresholding for each photograph and those obtained using automatic thresholding ($r = 0.958$–0.997, $P < 0.001$, $n = 64$). Automatic thresholding could not be used to analyse all hemispherical photographs, as on four occasions the presence of darker clouds led to misclassification of sky elements. In our final analyses we therefore used the mean variables from the estimates of two people calculated using manual thresholding.

The degree to which the CII can be related to each light availability variable (visible sky, ISF, DSF, GSF and LAI) was assessed firstly using Spearman's rank correlation. Secondly, the Kruskal–Wallis H-test was used to detect whether variables differed significantly between classes. Finally, the Mann-Whitney U test was used to undertake specific comparisons between the variables associated with each CII class, to determine whether classes were significantly distinct from each other.

3. Results

The mean proportion of visible sky, ISF, DSF and GSF all increased with crown illumination index class, with statistically significant positive correlations between the CII and each variable (Table 3). Also, the Kruskal–Wallis H-test highlighted significant differences in the visible sky, ISF, DSF and GSF associated with CII classes ($H = 32.92$, 37.98, 38.29 and 38.27, respectively, $P < 0.001$). The four lower classes (1, 1.5, 2 and 2.5) are more narrowly defined, which leads to a greater likelihood of overlap in these results. However, for ISF, DSF and GSF, classes 3 and 4 are significantly different from all others (Mann–Whitney U-test, $P < 0.05$) (Fig. 2, Table 3). The greater array of light levels encompassed in classes 3 and 4 is demonstrated by the generally larger range of values, compared to the lower classes.

There is a significant negative correlation between LAI and CII ($r_s = -0.634$, $P < 0.001$), with the mean LAI for each class decreasing consecutively (Table 3, Fig. 2e) and the Kruskal–Wallis H-test significant ($H = 33.02$, $P < 0.001$). However, the CII classes are less clearly defined using LAI, with no significant difference between classes 1, 1.5 and 2, or between 3 and 4.

We found a good degree of repeatability in CII classification, both between observers and by a single observer over time, in our separate study of the CII associated error, based on the assessment of trees at Sucusari. Two independent observers gave the same class or one class different on 91% of occasions ($n = 54$, Kendall's tau of concordance 0.934, $P = 0.0001$). Where classes differed, nearly 70% was by only 0.5, reflecting the narrow definition between classes at the lower end of the scale. Also, 86% of trees were given the same class or one

Table 3
Calibration results showing mean, standard error of the mean, minimum and maximum values of visible sky, indirect site factor (ISF), direct site factor (DSF), global site factor (GSF) and leaf area index (LAI) for each CII class

CII	1	1.5	2	2.5	3	4	r_s
Visible sky							
Mean	0.043	0.051	0.057	0.088	0.212	0.368	
S.E.	0.003	0.004	0.002	0.015	0.049	0.043	0.687*
Min	0.031	0.023	0.044	0.049	0.041	0.263	
Max	0.062	0.105	0.066	0.197	0.395	0.462	
ISF							
Mean	0.066	0.080	0.091	0.127	0.294	0.538	
S.E.	0.005	0.007	0.003	0.015	0.057	0.058	0.743*
Min	0.046	0.037	0.068	0.081	0.074	0.391	
Max	0.098	0.162	0.113	0.235	0.472	0.647	
DSF							
Mean	0.085	0.111	0.126	0.157	0.335	0.686	
S.E.	0.007	0.010	0.006	0.015	0.050	0.086	0.741*
Min	0.059	0.046	0.075	0.121	0.121	0.436	
Max	0.155	0.219	0.167	0.284	0.470	0.857	
GSF							
Mean	0.083	0.108	0.123	0.154	0.331	0.671	
S.E.	0.007	0.010	0.006	0.015	0.050	0.084	0.742*
Min	0.058	0.046	0.074	0.117	0.116	0.431	
Max	0.149	0.213	0.159	0.279	0.458	0.787	
LAI							
Mean	5.064	4.908	4.863	4.297	2.853	1.801	
S.E.	0.123	0.129	0.075	0.192	0.379	0.364	−0.634*
Min	4.272	3.509	4.367	3.291	1.685	1.339	
Max	5.768	5.888	5.471	5.121	4.069	2.881	

Visible sky, ISF, DSF and GSF are all given as proportions. r_s is the Spearman's rank correlation coefficient.
* Significant at $P < 0.001$.

different by one observer at the beginning and end of a 2-week period ($n = 111$, Kendall's tau of concordance 0.866, $P < 0.0001$). The CII classification of sampling locations in the calibration study (i.e. the hemisphere above the digital camera position), was more straightforward than that for trees in the CII associated error study. In contrast to the assessment of tree canopy light environments which are many metres above the forest floor and often obscured by other trees, there was clear visibility of the forest overstorey above the digital camera.

4. Discussion

This study provides the first complete calibration for crown illumination classes 1–4, and shows CII to vary closely with the proportion of visible sky and the site factors. The proportion of visible sky (i.e. the proportion of canopy containing gaps) is directly relevant to the CII assessment procedure since a visual estimation of the canopy gaps influencing a particular tree is used to assign index scores. Consequently, the values measured in this Amazonian forest provide a useful, quantitative calibration for this subjective measure. For example, where a tree canopy is classified as 1.5 (low lateral light) this indicates that gaps exist in 5.1 ± 0.4% (mean ± S.E.) of the canopy hemisphere 0–90° from the zenith angle, whereas a score of 4 (complete vertical light with no or some lateral light) suggests gap coverage of 36.8 ± 4.3%. Our results are consistent with the strong positive correlation found between CII and the proportion of visible sky (or ''canopy openness'') calculated by Davies et al. (1998) ($r_s = 0.82$) in a Bornean rain forest. Davies et al. (1998) found all classes to be significantly different (Table 2), however their study did not subdivide classes 1 and 2. Poorter and Arets (2003) also investigated the proportion of canopy openness related to each CII class in Amazonian Bolivia, but, unlike our Peruvian study, found no significant differences in the mean value of classes 1.5, 2 or 2.5 (Table 2).

The calculated site factors also provide useful information describing the typical light environment of each index class, with strong correlations found between CII and ISF, DSF and GSF. Our findings parallel those of Clark and Clark (1992) who noted strong correlations between CII and ISF and DSF ($r_s = 0.87$ and 0.83, respectively, $P < 0.01$). In our study, a tree anopy with a CII of 4 has on average 67.1 ± 8.3% of the total available light above the canopy, more than eight times as much available light as a tree with a CII of 1, which receives only 8.3 ± 0.7%. This may therefore help to explain a great deal about an individual tree's life dynamics and suggests that we should not expect photosynthetic and growth rates to be linearly related to CII. These results significantly improve on the previous calibration attempts using GSF (Clark et al., 1993), where correlation with CII was weaker ($r_s = 0.34$, $P < 0.001$) and DSF (Poorter and Arets, 2003) where estimates were not available for all CII classes (Table 2).

This study is the first attempt to calibrate CII with respect to leaf area index. Although average LAI did decrease consecutively with increasing CII, there is considerable overlap in the LAI values associated to each CII class. This may be due to the greater error inherent in estimating LAI using indirect methods (Whitford et al., 1995; Jonckheere et al., 2004). The method of calculation is more complex than that used for other variables calculated within this study, with LAI values potentially underestimated to some extent due to the necessary assumption of random foliage distribution (Lang and Xiang, 1986; Chen and Cihlar, 1995; Leblanc et al., 2005). Therefore, where the different classes within the CII are closely associated (i.e. classes 1–2.5), calculation errors may outweigh any small differences in actual leaf area index. Consequently, while our results provide some information concerning coarse-scale variation in leaf area index with CII, more precise calibration of CII with respect to LAI may prove challenging.

The interpretation of CII classes is designed to be invariant with forest type, and so our results for the proportion of visible sky and LAI should have general applicability across difference forest structures and compositions. However, the mean values for each variable estimated in this study are not always consistent with those calculated in other studies. For example, the mean visible sky values reported by Poorter and Arets (2003) and by Davies et al. (1998) tend to be lower than those calculated in this study for the equivalent CII class. This may reflect methodological differences, including thresholding methods or subjectively different interpretations of the index. One way to ensure that the subjective, observer effect is reduced would be to train investigators in the use of CII using these

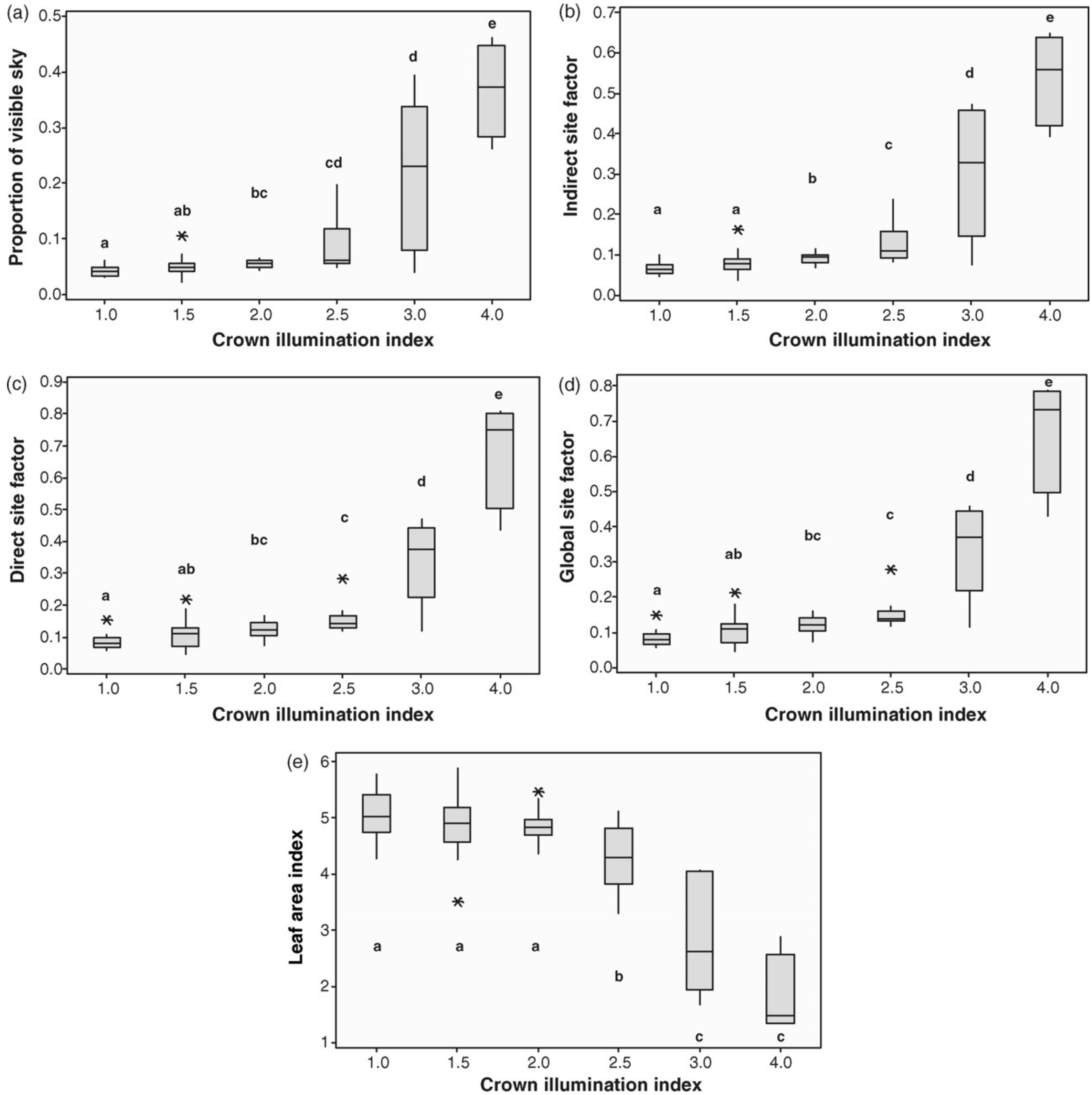

Fig. 2. Box plots of (a) proportion of visible sky, (b) indirect site factor (ISF), (c) direct site factor (DSF), (d) global site factor (GSF) and (e) leaf area index (LAI), for each crown illumination index class. Boxplots show 25% quartile, median and 75% quartile of the distributions (horizontal lines); vertical lines extend a further 1.5 times the interquartile (25–75%) range; *denotes outlier. (a–e) Significant differences (Mann–Whitney U-test, $P < 0.05$).

calibrations. Along with the qualitative class descriptions, the average and range of proportion of visible sky for each class should help the investigator to understand how to operationalize statements such as ‘‘low’’, ‘‘medium’’ and ‘‘high’’ lateral light. Also, the sharing of ‘‘typical’’ hemispherical photographs representing each class (e.g. Fig. 1) may help ensure that observer interpretations of each CII class converge.

5. Conclusions

The indirect, direct and global site factors provide the strongest correlations with CII, as well as containing the least overlap between classes. The proportion of visible sky also offers a practical means of calibration, which is applicable across tropical sites. The success of this calibration substantiates claims of field ecologists that CII can provide an efficient and effective method for rapidly describing forest light environments.

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References

Chazdon, R.L., Fetcher, N., 1984. Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. J. Ecol. 72, 553–564.

Chen, J.M., Cihlar, J., 1995. Plant canopy gap-size analysis theory for improving optical measurements of leaf-area index. Appl. Optics 34, 6211–6222.

Clark, D.A., Clark, D.B., 1992. Life history diversity of canopy and emergent trees in a neotropical rainforest. Ecol. Monogr. 62, 315–344.

Clark, D.B., Clark, D.A., Rich, P.M., 1993. Comparative-analysis of microhabitat utilization by saplings of 9 tree species in neotropical rain-forest. Biotropica 25, 397–407.

Cutini, A., Matteucci, G., Mugnozza, G.S., 1998. Estimation of leaf area index with the Li-Cor LAI 2000 in deciduous forests. For. Ecol. Manag. 105, 55.

Davies, S.J., Ashton, P.S., 1999. Phenology and fecundity in 11 sympatric pioneer species of *Macaranga* (Euphorbiaceae) in Borneo. Am. J. Bot. 86, 1786–1795.

Davies, S.J., Palmiotto, P.A., Aston, P.S., Lee, H.S., Lafrankie, J.V., 1998. Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. J. Ecol. 86, 662–673.

Dawkins, H.C., Field, D.R.B., 1978. A Long-term Surveillance System for British Woodland Vegetation. Department of Forestry, Oxford University, Oxford.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., Baret, F., 2004. Review of methods for in situ leaf area determination. Part I. Theories, sensors and hemispherical photography. Agric. For. Meteorol. 121, 19–35.

King, D.A., Davies, S.J., Supardi, M.N.N., Tan, S., 2005. Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. Funct. Ecol. 19, 445–453.

Kobe, R.K., 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. Ecology 80, 187–201.

Lang, A.R.G., Xiang, Y., 1986. Estimation of leaf area index from transmission of direct sunlight in discontinuous canopies. Agric. For. Meteorol. 37, 229–243.

Leblanc, S.G., Chen, J.M., Fernandes, R., Deering, D.W., Conley, A., 2005. Methodology comparison for canopy structure parameter extraction from digital hemisphercial photography in boreal forests. Agric. For. Meteorol. 129, 187–207.

Malhi, Y., Phillips, O.L., Lloyd, J., Baker, T., Wright, J., Almeida, S., Arroyo, L., Frederiksen, T., Grace, J., Higuchi, N., Killeen, T., Laurance, W.F., Leano, C., Lewis, S., Meir, P., Monteagudo, A., Neill, D., Vargas, P.N., Panfil, S.N., Patino, S., Pitman, N., Quesada, C.A., Rudas-Ll, A., Salomao, R., Saleska, S., Silva, N., Silveira, M., Sombroek, W.G., Valencia, R., Martinez, R.V., Vieira, I.C.G., Vinceti, B., 2002. An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). J. Veg. Sci. 13, 439–450.

Malizia, A., Grau, H.R., 2006. Liana-host tree associations in a subtropical montane forest of north-western Argentina. J. Trop. Ecol. 22, 331–339.

Miller, J.B., 1967. A formula for average foliage density. Aust. J. Bot. 15, 141–144.

Nobis, M., Hunziker, U., 2005. Automatic thresholding for hemispherical canopy-photographs based on edge detection. Agric. For. Meteorol. 128, 243–250.

Oberbauer, S.F., Clark, D.B., Clark, D.A., Rich, P.M., Vega, G., 1993. Light environment, gas-exchange, and annual growth of saplings of 3 species of rain-forest trees in Costa-Rica. J. Trop. Ecol. 9, 511–523.

Poorter, L., Arets, E., 2003. Light environment and tree strategies in a Bolivian tropical moist forest: an evaluation of the light partitioning hypothesis. Plant Ecol. 166, 295–306.

Saenz, G., Finegan, B., Guariguata, M., 1999. Sapling growth and mortality of seven tree species in an altered very moist tropical forest, Costa Rica. Rev. Biol. Trop. 47, 45–57.

Sheil, D., Salim, A., Chave, J.R., Vanclay, J., Hawthorne, W.D., 2006. Illumination-size relationships of 109 coexisting tropical forest tree species. J. Ecol. 94, 494–507.

Singhakumara, B.M.P., Gamage, H.K., Ashton, M.S., 2003. Comparative growth of four *Syzygium* species within simulated shade environments of a Sri Lankan rain forest. For. Ecol. Manag. 174, 511–520.

Sterck, F.J., Clark, D.B., Clark, D.A., Bongers, F., 1999. Light fluctuations, crown traits, and response delays for tree saplings in a Costa Rican lowland rain forest. J. Trop. Ecol. 15, 83–95.

Svenning, J.C., 2002. Crown illumination limits the population growth rate of a neotropical understorey palm (*Geonoma macrostachys*, Arecaceae). Plant Ecol. 159, 185–199.

van Gardingen, P.R., Jackson, G.E., Hernandez-Daumas, S., Russell, G., Sharp, L., 1999. Leaf area index estimates obtained for clumped canopies using hemispherical photography. Agric. For. Meteorol. 94, 243–257.

van Gelder, H.A., Poorter, L., Sterck, F.J., 2006. Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. New Phytol. 171, 367–378.

Vasquez, R., Phillips, O., 2000. Floristics, structure, and dynamics of a high diversity forest in Amazonian Peru. Ann. Mol. Bot. Gard. 87, 499–527.

Walters, M.B., Reich, P.B., 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. Ecology 77, 841–853.

Whitford, K.R., Colquhoun, I.J., Lang, A.R.G., Harper, B.M., 1995. Measuring leaf-area index in a sparse eucalypt forest—a comparison of estimates from direct measurement, hemispherical photography, sunlight transmittance and allometric regression. Agric. For. Meteorol. 74, 237–249.

Wright, E.F., Coates, D., Canham, C.D., Bartemucci, P., 1998. Species variability in growth responses to light across climatic regions in northwestern British Columbia. Can. J. For. Res. 28, 871–886.