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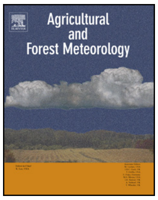

Comparison of direct and indirect methods for assessing leaf area index across a tropical rain forest landscape

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ABSTRACT

Many functional properties of forests depend on the leaf area; however, measuring leaf area is not trivial in tall evergreen vegetation. As a result, leaf area is generally estimated indirectly by light absorption methods. These indirect methods are widely used, but have never been calibrated against direct measurements in tropical rain forests, either at point or landscape scales. Here, we compare direct harvest leaf area index (LAI) measurements taken across an old-growth tropical rain forest landscape with data from two indirect methods, digital hemispherical photography and the LI-COR LAI-2000 Plant Canopy Analyzer. Direct measurements of leaf area were done by collecting all leaf material within an area of 4.6 m^2, extending from the forest floor to the top of the canopy using a portable aluminum scaffolding tower. The tower was erected at 45 locations following a stratified random design.

Mean direct-harvest LAI above 1 m was 5.5 ± 0.3 SE. Plant area index (PAI, leaves + wood) was 5.1 ± 0.2 for the LAI-2000, and for the hemispherical photographs was 3.9 ± 0.2, analyzed using Gap Light Analyzer (GLA), and 4.9–6.0 ± 0.2 using WinSCANOPY software. Correction for leaf clumping (non-random distribution of leaves) generally improved LAI estimates of the hemispherical photographs. At the local scale, direct-harvest LAI was not significantly correlated with LAI estimates for either indirect method. However, correlations between direct-harvest LAI and both indirect methods along vertical canopy transects from forest floor to the canopy top were significant. Relationships between harvest LAI and canopy closure (from which indirect LAI values are derived) showed very small changes in closure with large changes in LAI at LAI values > 6, indicating that the estimations of LAI using canopy closure values were reaching an asymptote. As a result, at high canopy closure indirect LAI is underestimated. Overall, the LAI-2000 performed better than hemispherical photography for estimating direct-harvest LAI at landscapes scales. However, with corrections for leaf clumping, hemispherical photography can be effective for estimating and characterizing landscape level LAI of tropical rain forest.

1. Introduction

Tropical rain forests (TRFs) play a key role in the global carbon cycle, storing ~60% of the world's aboveground forest biomass and ~27% of its soil carbon (Dixon et al., 1994; Phillips et al., 1998). The contribution of TRFs to the global net primary production (NPP) is estimated at 20–40%. However, NPP estimates vary considerably (Melillo et al., 1993; Phillips et al., 1998), in part as a result of the relatively few measurements of the structure and function of TRF, including leaf area index (LAI). LAI represents the interface between plants and the atmosphere, and is a fundamental parameter in models of ecosystem production. Processes of carbon uptake, transpiration, leaf respiration, and canopy interception are tightly coupled to leaf area. Furthermore, light availability, tree recruitment, and growth are strongly affected by total leaf area, as well as its vertical, temporal and spatial distribution (Chason et al., 1991;

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Moser et al., 2007). Therefore, reproducible measurements of LAI are required to understand the processes that drive TRF productivity (Moser et al., 2007), and the potential response of TRF to climate change.

For broadleaf canopies such as those in TRF, LAI (m^2 of leaves/m^2 of ground) is defined as the one-half of the total surface leaf area per unit ground area (Chen and Black, 1992; Jonckheere et al., 2004). Assessing LAI for TRF landscapes is particularly difficult because of the complex spatial arrangement of the leaves, gap dynamics, the presence of many evergreen species with different leaf life spans, and tall canopies. In temperate broadleaf deciduous forests, relatively robust estimates of LAI can be obtained using litterfall collections. In short canopies, such as grassland and tundra, LAI can be estimated using point quadrat methods (Warren Wilson and Reeve, 1959). Nevertheless, directly quantifying LAI in most forests is problematic because of temporal and spatial variation of LAI. Consequently, indirect methods of estimating LAI (Marshall, 1986; Ferment et al., 2001; Rhoads et al., 2004; Leblanc et al., 2005; Arias et al., 2007) have been widely adopted because of their versatility and ease of temporal and spatial replication. These methods include allometric relationships, gap-fraction (e.g., hemispherical photography), and light transmittance measurements with optical sensors (e.g., LI-COR LAI-2000 Plant Canopy Analyzer, or Decagon AccuPAR). However in many tall forest ecosystems including TRF, indirect methods have not been calibrated against direct measures of LAI because of the difficulty in obtaining replicated direct measurements.

Each of the methods used to indirectly determine LAI has a different set of limitations that can affect the estimates. Allometric equations require detailed information for every location because they are sensitive to species composition and forest structure (Gower et al., 1999; Leblanc et al., 2005; Arias et al., 2007). Optical (gap fraction and transmittance) sensors cannot distinguish between the light intercepted by leaves and woody structures (Gower et al., 1999; Rhoads et al., 2004; Kalacska et al., 2005b). Therefore, unless corrected for wood area, the optical sensors estimate the plant area index (PAI, leaves, branches and stems) and not the LAI. Moreover, optical measurements are sensitive to sky conditions; ideally they should be taken under diffuse light (Nackaerts et al., 2000). Transmittance measurements, such as the LAI-2000, require a reference measurement above or outside the canopy, presenting a serious challenge in closed and tall forests. Of the indirect methods used to estimate LAI, hemispherical photography is often logistically the simplest approach. However, analysis may involve subjective determination of canopy closure or openness, which may be particularly difficult under dense canopies with many overlapping layers of leaves.

The height and complex vertical structure of TRF makes direct assessments of LAI both difficult and expensive. Few direct measurements of LAI have been made in TRF, and calibration of the optical methods at the landscape level has not been attempted (Moser et al., 2007). Here we report the results of a comparison of directly measured LAI with two indirect methods of LAI estimation: light transmission measurements with the LI-COR LAI-2000 and hemispherical photography. Comparisons were made across a TRF landscape to address three questions: (1) How well do indirect methods estimate LAI at the landscape level? (2) Are there systematic differences between the indirect methods? (3) How do indirect methods perform at estimating cumulative direct-harvest LAI at different heights within the canopy?

Because of the large differences in footprint/field of view, we do not expect significant relationships between the direct harvest and the indirect methods at the local scale. Therefore, the work presented here seeks to determine the ability of indirect methods to estimate LAI of a forest at the landscape level.

2. Methods and materials

2.1. Study site and sample design

This study was conducted in 2003 and 2004 at La Selva Biological Station, located in the Caribbean lowlands of northern Costa Rica, Central America (10°26′ N, 83°59′ W). The forest is tropical wet forest, with annual precipitation of ~4000 mm, and annual mean temperature of ~26 °C. The old growth averages 446 trees ha^{-1} (≥10 cm diameter at breast height) with an average basal area of 25 m^2 ha^{-1} (Lieberman and Lieberman, 1987). Our study area was upland (terra firme) old growth. Previous studies at La Selva indicate that soil phosphorus (Espeleta and Clark, 2007; D.A. Clark and D.B Clark, unpublished data) and slope (Clark and Clark, 2000) are important determinants of forest structure. Therefore, the 45 sampling sites were selected using a stratified random design with estimated soil phosphorus (0–10 cm depth) and slope as block variables (Supplement Fig. 1). Detailed description of the sampling design can be found in Clark et al. (2008).

2.2. Direct LAI estimation

A walk-up aluminum scaffolding tower consisting of stackable sections was used to perform a destructive collection of all leaf and woody material (branches and trunks <10 cm DBH) from the forest floor to the top of the canopy at intervals of 1.9 m (the height of a tower section). The collected material represented the leaf and woody materials distributed along a vertical column with horizontal area of 4.6 m^2, where LAI and wood area index (WAI) can be determined at different forest heights (see Clark et al., 2008 for details). All leaf and woody harvested material was brought to the laboratory where the area was carefully measured. Leaf area was determined by measuring each harvested leaf with a leaf area meter LI-3100C (LI-COR Inc., Lincoln, NE, USA). Woody material was measured for length and diameter to calculate surface wood area. The leaf and woody areas were grouped by location and height (see below for further detail). Canopy height ranged from 3 to 45 m, with a mean height of 27.2 ± 1.1 SE.

Direct-harvest LAI was determined by adding all leaf area within a tower section and summing up all sections to get the total leaf area at each location. Measurement of the leaf area by tower section allowed the determination of the cumulative LAI at different heights within the canopy. Woody area was calculated as one-half of the total surface area of the harvested wood segments found within each tower section, and total WAI was calculated as the sum of the surface area of all branches and stems found within the vertical transect (tower). To compare the direct harvesting results with those of the indirect methods that were taken at 1 m height, 50% of the foliage/wood harvested in the first 1.9 m was subtracted from the LAI and WAI totals. This modified harvested values of LAI and WAI used for comparisons are referred to as LAI_{1m} and WAI_{1m}.

Additionally, to estimate the WAI of the trunks, tree plots were surveyed at each location. In a ~314 m^2 plot, all trees with a diameter larger than 10 cm at breast height (DBH) were measured. Tree height was estimated using an allometric equation developed by Feldpausch et al. (2011) for continental South America, $\log(H) = \beta_0 + \beta_1 \log(D)$ where H is the tree height in meters, and β_0 (1.3760) and β_1 (0.4854) are coefficients and D in the diameter in cm. The WAI of trunks was estimated by summing half of the total surface area of all the trees in the plots and dividing it by the area of the plot. Here we report the WAI of trunks for the forest. However, it is important to clarify that because no towers were built in areas with trees larger than 10 cm, no relationships between WAI (for trees lager 10 cm trunks) and LAI was estimated. Therefore, the WAI used for correcting the indirect methods took into account only branches and trunks less than 10 cm.

2.3. Indirect LAI estimation

Leaf area index was indirectly assessed on 44 of the 45 tower sites with two widely used optical methods: hemispherical photography (Nikon Coolpix 4500 with FC-E8 0.21x hemispherical lens, Nikon USA, Melville, NY, USA, only zenith angles 0–60° were used) and the Plant Canopy Analyzer (LAI-2000, LI-COR Inc., Lincoln, NE, USA). Inclement weather prevented indirect measurements of LAI at one of the tower locations.

Before any leaf or wood harvesting was begun at a tower location a color hemispherical photograph was taken in the center of the sampling area (tower footprint). At each height (tower section), before harvest and a section of the scaffolding tower was put up, another image was taken. The images were taken at 1 m height above the forest floor and subsequently at intervals of 1.9 m. The camera was always leveled and oriented in the same direction, so that the top of the image was directed north. Images were 1024×768 pixels or higher resolution. We avoided taking photographs under direct beam sun conditions whenever possible, but as a result of the tower construction schedule, bright conditions occurred in some images (38% of the cases). We used two programs to analyze the hemispherical images: Gap Light Analyzer (GLA v2; Frazer et al., 2000), and WinSCANOPY (Version 2006a Pro, Régent Instruments Inc.). GLA was used for analysis of images from all locations and canopy levels; WinSCANOPY was only available for analysis of images taken at the forest floor.

GLA calculates PAI based on a threshold value used to classify pixels as canopy components (black for foliage and wood) or open space (white). The threshold was determined as the average of two visual classifications by a single operator. We used the output variables percent canopy openness and LAI 4-ring. LAI 4-ring represents the effective estimated LAI integrated over zenith angles of 0–60°. However, this approach has limitations because leaf clumping (non-random distribution of leaves in the image) may cause underestimation of LAI (Leblanc et al., 2005).

WinSCANOPY software uses color pixel classification to determine the threshold for binary pixel conversion. For the analysis, images were divided into similar light conditions, and then a color classification was done based on sky and foliage, thereby avoiding subjectivity in the calculation of LAI. Although WinSCANOPY output includes LAI estimates using several methods (see Supplement Table 1), here we analyzed only the lowest and highest values. On average, the lowest LAI was obtained using the LAI-2000 generalized log method (2000G), similar to the method used to process the LAI-2000 readings (Welles and Norman, 1991). The highest LAI estimates were obtained with the spherical method. A detailed description of the different methods and outputs in WinSCANOPY can be found at http://www.regent.qc.ca/products/Scanopy/SCANOPYSoftware.html.

Both indirect methods (LAI-2000 and hemispherical photographs) assume that leaves and gaps are randomly distributed in the canopy. These assumptions are rarely met and have been addressed with the development of several indices (Welles and Norman, 1991; Leblanc, 2002; Leblanc et al., 2005) that compensate for non-random distribution of gaps (large openings) and leaves (clumping). WinSCANOPY accounts for non-random or discontinuous canopies using a clumping index (CI). The clumping index is a theoretical relationship between the quantity of gaps among crowns (large non-random gaps) and the quantity of gaps within crowns (small and random gaps). Values close to 1 indicate that the gaps and the foliage in the canopy are randomly distributed, whereas lower values represent some degree of clumping. Clumping index can be used in two ways: (1) dividing estimated LAI by a clumping index calculated from the entire image, (2) subdividing the image into different ranges of zenith angles and applying a separate clumping index to each range to correct the LAI, as is done in the 2000G and spherical methods. To improve comparison of LAI estimates made by the two software programs, the highest and lowest clumping indexes obtained from WinSCANOPY were used to recalculate mean estimated LAI from the GLA analysis.

After tower construction was completed, LAI was estimated at the forest floor and at each tower section using two cross-calibrated, time-synchronized LAI-2000 instruments (Welles and Norman, 1991). Measurements were carried out under diffuse-light conditions. One instrument was placed at the top of the tower above the canopy logging incoming light every 15 s on the undisturbed side of the tower (opposite from where tower sections were lifted). The second instrument was used to take readings at each tower section in the same side of the tower. Both sensors were fitted with a 180° view cap over the lens half closest to the tower, minimizing any influence of the tower on the lower sensor. At the ground level two assessments were made: a single measurement at the base of the tower at 1 m height, and a five-point transect with 5 m spacing perpendicular to undisturbed side of the tower.

Data from the two LAI-2000 instruments were merged using LI-COR C2000 software (Welles and Norman, 1991), resulting in a vertical profile of LAI at 1.9 m intervals from the forest floor (1 m) to the top of the canopy. To estimate total LAI (above 1 m) at each site, we compared the single reading at the base of the tower and the average of the five-point transect extending away from the tower base. However, no significant difference was found between these two approaches (two-tail t-test, $N = 43$, $t = -0.904$, $p = 0.371$), and we report only the single-point results. This finding is probably a consequence of spatial autocorrelation of canopy structure (Clark et al., 1996).

2.4. Correction of optical estimates for wood area index

We used the direct-harvest values of WAI (from branches and trunks less than 10 cm DBH) to correct for the effect of woody area on optical PAI measurements. Although harvested WAI does not account for all the wood present in the images such as the large trunks, it represents a reasonable estimate of the leaf to wood ratio present in the vertical transect, allowing for the estimation of the LAI in the images. WAI was established as the proportion of wood area to PAI for each site. This ratio was used to determine the adjusted leaf area index (LAI_{adj}) for both optical methods. LAI_{adj} was calculated as:

$$\text{LAI}_{\text{adj}} = \text{PAI}^* \left(1 - \left(\frac{\text{WAI}_{1\text{m}}}{\text{PAI}_{1\text{m}}}\right)\right) \qquad (1)$$

where LAI_{adj} is the LAI adjusted for wood area, PAI is the value obtained from uncorrected hemispherical photographs or LAI-2000 measurements, and $\text{WAI}_{1\text{m}}$ and $\text{PAI}_{1\text{m}}$ are the wood area index and plant area index obtained from direct harvesting.

2.5. Canopy vertical LAI profiles

The vertical LAI profile constructed by calculating the cumulative direct-harvest LAI from the top-down at each tower section was compared against the LAI_{adj} obtained with the LAI-2000 and hemispherical photographs (GLA). This approach allowed assessment of the performance of each indirect method in estimating the direct-harvest LAI over a wide range of values as it accumulates with increasing distance from the top of the canopy (canopy depth).

Because optical estimates of LAI are derived from measures of canopy closure (or from openness), we evaluated the relationships between optically determined canopy closure (LAI-2000 and GLA) and direct-harvest LAI at different forest heights. This approach

Table 1

Plant area index (PAI), Adjusted LAI (LAI$_{adj}$) after correction for wood area (WAI) and clumping, percent coefficient of variation (CV), percent deviation from the direct-harvest LAI$_{1m}$ (measurements taken at 1 m) estimated using the LAI-2000, GLA, and WinSCANOPY, and *p* value of a paired *t*-test against LAI$_{1m}$.

Method	PAI	LAI$_{1m}$ or LAI$_{adj}$	CV (%)	Percent deviation	*p* value
Direct harvesting (LAI$_{1m}$)	5.95 ± 0.4	5.54 ± 0.3	*40*		
LAI-2000_base	5.1 ± 0.2	4.56 ± 0.1[a]	22	−18	0.003
Photo (GLA)	3.9 ± 0.2	3.45 ± 0.1[a]	24	−38	0.001
Photo (GLA, CI 0.71)	3.9 ± 0.2	4.9 ± 0.2[b]	24	−12	0.068
Photo (GLA, CI 0.82)	3.9 ± 0.2	4.2 ± 0.2[b]	24	−24	0.001
Photo (WinSCANOPY, lowest LAI)	4.9 ± 0.2	4.4 ± 0.2[b]	24	−21	0.001
Photo (WinSCANOPY, highest LAI)	6.0 ± 0.2	5.4 ± 0.2[b]	25	−3	0.633

[a] Corrections using WAI.

[b] Corrections with WAI and CI.

allowed determination of the effect that increments in cumulative direct-harvest LAI have on canopy closure and which method (LAI-2000 or GLA) best detects these changes. For photographic methods, canopy closure can be derived from openness, which is a standard output. For the LAI-2000, the percent canopy closure was calculated using the Beer–Lambert law with an extinction coefficient (k) of 0.5 (Gower et al., 1999; Kitajima et al., 2005). The data used were the uncorrected data (PAI), because the goal was to determine total closure regardless of which canopy component was obstructing the light (leaves, stems, branches).

2.6. Data analysis

Estimates of LAI were compared against the direct-harvest LAI using a paired *t*-test comparison of means using the one-tailed approach. A logarithmic regression was fitted to harvested LAI and canopy closure.

3. Results

3.1. Comparison of LAI estimates among methods

The landscape average total canopy LAI (6.0 ± 0.3 SE, Clark et al., 2008) adjusted to LAI above 1 m (LAI$_{1m}$) was 5.5 ± 0.3. Wood area index by direct harvest totaled 0.67 ± 0.1 and was linearly correlated with harvested LAI$_{1m}$ ($R^2_{adj} = 0.35$, $N = 44$, $p < 0.001$). The WAI of trunks was 0.4 ± 0.02 (index not used for corrections of indirect methods). When PAI determined by indirect methods was corrected with the harvest WAI$_{1m}$ at each location, mean LAI$_{adj}$ was 4.6 ± 0.1 for the LAI-2000, 4.4 ± 0.2–5.4 ± 0.2 for WinSCANOPY analysis, and 3.4 ± 0.1 for GLA analysis (Table 1). The contribution of wood to PAI estimates was ~11% for the three indirect approaches.

Photo analysis by WinSCANOPY compensates for nonrandom leaf distribution in the images with a clumping index (CI). Clumping indices ranged from 0.71 to 0.82, depending on the approach (Supplement Table 1). When the highest and lowest CI from WinSCANOPY were applied to LAI$_{adj}$ estimate from GLA, LAI$_{adj}$ ranged increased to 4.2–4.9, respectively.

Overall, direct-harvest LAI$_{1m}$ at the tower was underestimated by LAI$_{adj}$ of the LAI-2000 by 18%, WinSCANOPY 2000G by 21%, WinSCANOPY Sphere by 3%, and GLA corrected for high and low leaf clumping by 12% and 24%, respectively (Table 1). All methods except for WinSCANOPY Sphere and GLA low leaf clumping index were significantly different from direct-harvest LAI$_{1m}$ (Table 1).

As expected at the local basis, the direct-harvest LAI measurements were not significantly correlated with indirect measurements ($R^2_{adj} = 0.06$, -0.02, and 0.01, for LAI$_{adj}$ from the LAI-2000, LAI$_{adj}$ from the GLA analysis, and for both estimates from WinSCANOPY, respectively). Values from the LAI-2000 and hemispherical photographs were also not strongly correlated; only WinSCANOPY Sphere LAI$_{adj}$ was positively related with LAI$_{adj}$ determined by the LAI-2000 ($R^2_{adj} = 0.1$, $p < 0.026$). LAI$_{adj}$ from the GLA analysis and the two estimates from WinSCANOPY were significantly related ($R^2_{adj} = 0.72$ and 0.61 for 2000G and Sphere methods, respectively, $p < 0.001$).

3.2. Canopy vertical profile

We compared the cumulative direct-harvest LAI against the LAI$_{adj}$ (corrected only for WAI) from the LAI-2000 and the GLA analysis along the vertical canopy profiles (Fig. 1). In the upper canopy all methods performed similarly, but as cumulative harvest LAI increased from the top-down, it was underestimated by LAI$_{adj}$, starting at LAI harvest values ~2 for the GLA analysis and ~4 for the LAI-2000 (Fig. 1). Regressions across the vertical transect between direct-harvest LAI and LAI$_{adj}$ of the indirect methods showed exponential relationships. Even after controlling for the direct relation between LAI and height, square root-transformed direct-harvest and indirect methods were significantly related ($R^2_{adj} = 0.31$ and 0.29, $p < 0.0001$ for the LAI-2000 and GLA photo analysis, respectively).

3.3. Canopy closure

Regressions between cumulative direct-harvest LAI and canopy closure from the LAI-2000 and GLA photo analysis were logarithmic and significant ($R^2 = 0.53$ and 0.32, $p < 0.0001$ for both, respectively). However as closeness approached ~80%, LAI derived from canopy closure failed to detect large changes in LAI. This was observed for values >4 for hemispherical photographs and > 6 for the LAI-2000.

4. Discussion

4.1. Comparison among methods

This study provides the first calibrations for indirect methods of LAI measurement based on comparisons with direct harvesting in TRF. At the landscape level, the LAI-2000 values and hemispherical photo analyses without correction for leaf clumping significantly underestimated the LAI determined using direct harvest (Table 1). Correction for WAI exacerbated the underestimates; for the LAI-2000, underestimates increased from 8% to 18%. Previous studies in northern deciduous forest found that the LAI-2000 underestimated the leaf area index determined with litter traps by 14% (Rhoads et al., 2004) to 26% (Cutini et al., 1998). In tropical dry forest, Kalacska et al. (2005a,b) found that the LAI calculated with the LAI-2000 was 17–40% lower than LAI estimated using litter fall traps.

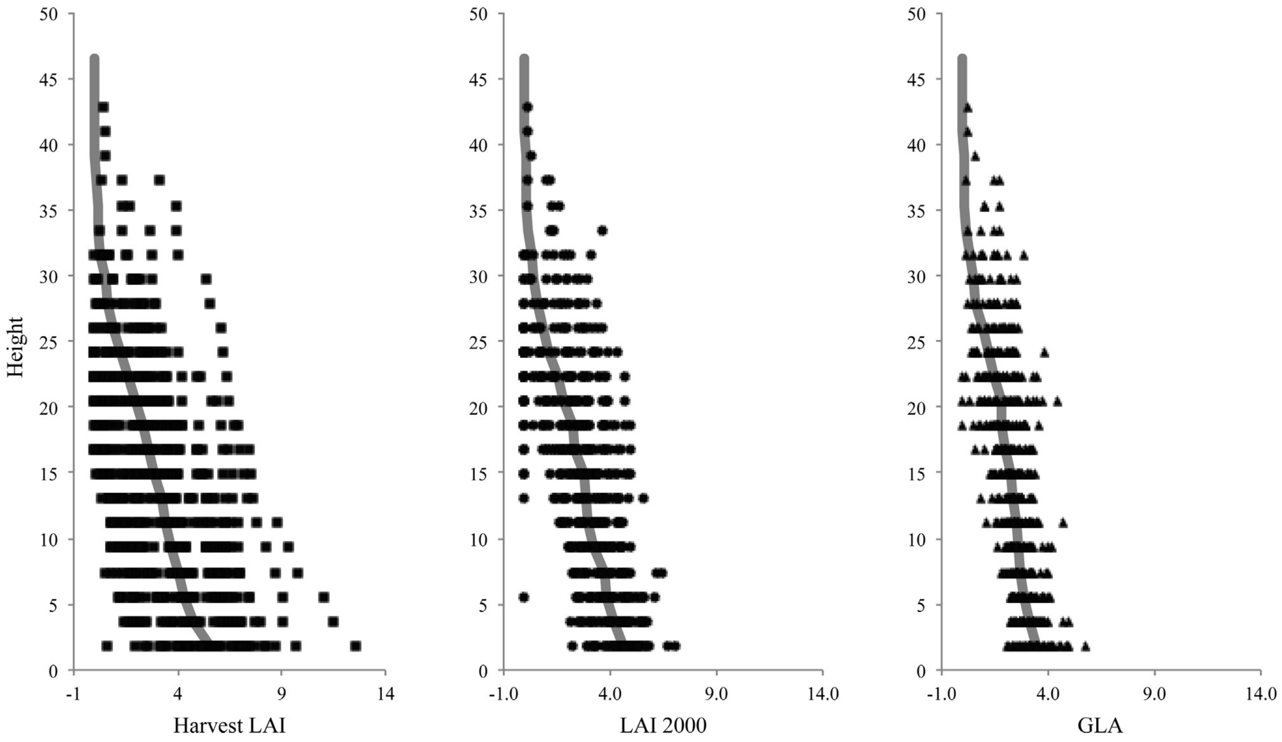

Fig. 1. Relationships between canopy height and LAI measured with direct harvest, LAI 2000, and hemispherical photographs. Solid lines represent mean vertical profile ($N = 44$) of cumulative LAI and points represent the LAI at different canopy heights and locations. Indirect methods were corrected using the mean WAI for each height.

Correction of hemispherical photo estimates for leaf clumping strongly reduced the underestimation of harvest LAI. WinSCANOPY analyses of hemispherical photos, which include a correction for leaf clumping, were close to the direct-harvest values before correction for WAI, ranging from an overestimation of 9% to an underestimation of 12%, and with WAI correction, underestimates of 3% and 21%, respectively.

Estimates of LAI from photographs analyzed with GLA were the most different from the direct-harvest measurements of LAI, underestimating LAI_{1m} by 30%. With correction for WAI, the underestimate was 38%. Application of CI to the GLA LAI_{adj} reduced the percentage of LAI underestimation from 38% to between 12% and 24%, depending on the CI used, values approaching those obtained from WinSCANOPY. The superior performance of WinSCANOPY may be a result of correcting for clumping at each zenith angle by the methods used (2000G and Sphere), rather than using a single global image correction, as was applied here to GLA analysis.

However, even with direct measurement of LAI, calibration of indirect optical methods is not straightforward because the scale of optical measurements is typically much larger than that possible by direct assessments. This difference is reflected in both the coefficients of variation for the different approaches and the lack of significant correlations between point-to-point comparisons of the indirect measurements and direct-harvest LAI_{1m} (Rhoads et al., 2004). Although low (CV = 40%), the horizontal variation of LAI at the relatively small scale of the tower footprint (4.6 m^2) was much greater than the variation observed with the larger scale (hectares) optical assessments (Table 1). For the hemispherical photos, the leaf area harvested in the LAI_{1m} estimate was only a small fraction of the field of view of the camera. The LAI-2000 was used after the vertical column was harvested, so the sampling areas of the two methods did not overlap. Furthermore, because we used the 180° view cap on the LAI-2000, the hemispherical photos only shared half of the field of view with the LAI-2000. Despite the smaller field of view, the LAI-2000 had slightly lower CV than that of the photos, suggesting that it provides the better measurement in heterogeneous canopies.

4.2. WAI

If the objective of using optical methods is to simply measure light conditions (gap fraction, canopy closure or openness) beneath a forest canopy, the light obstructed by trunks and branches is not of concern and the use of PAI may be adequate. However, if the objective is to estimate the leaf area, the fact that the LAI-2000 and hemispherical photographs do not distinguish between wood and leaves has to be considered. Our WAI approach was intended to approximate the influence of light intercepted by wood on estimates of LAI by indirect methods taking into account only branch and small trunk areas. We found a positive relationship between wood and leaf area using direct-harvest methods. The ratio of wood to plant area was ∼11% of PAI. Although the WAI in our sampling method did not include large tree trunks and therefore represents an underestimate, the ratio can be used to correct for wood area in indirect measurements (Norman and Jarvis, 1975). Because no vertical transects were constructed on top of trunks larger than 10 cm DBH, the WAI of trunks was not included in the WAI-PAI relationship from the direct harvest to prevent bias toward wood area. Nevertheless, we found that the WAI of the trunks was 0.4 ± 0.02. Additionally, our WAI approach assumes all branches and trunks to be horizontal (similar to the estimation of LAI), providing an upper estimate of the total area occupied by wood.

Unlike in deciduous forests, where light interception by wood can be measured when the canopy is leafless during the cold or dry season (Cutini et al., 1998; Soudani et al., 2001; Kalacska et al., 2005a), the abundance of evergreen species in TRF makes determination of light interception by wood a serious challenge. Cutini et al. (1998) found a WAI of 0.8 in undisturbed deciduous forest stands; when the raw LAI-2000 values were corrected for WAI, the underestimation of litter trap LAI increased from 26.5% to 39.4%.

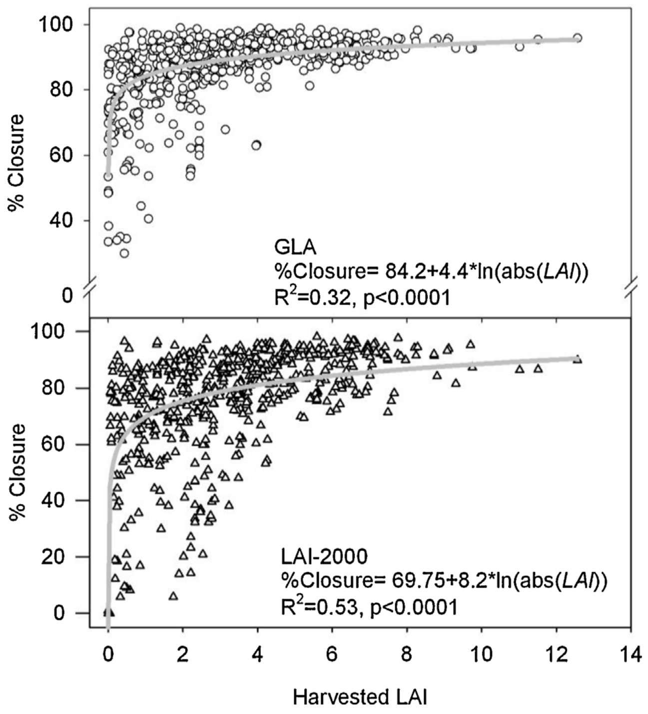

Fig. 2. Relationship between canopy closure and cumulative direct-harvest LAI at all locations and forest heights (sections and towers). LAI-2000 upper panel ($R^2_{\text{adj}} = 0.53$), GLA lower panel ($R^2_{\text{adj}} = 0.32$). Because of differences in footprint of the harvested LAI and the indirect measurements, it was possible to encounter situations where canopy closure of 0% was not matched with LAI of 0 and to find points with a LAI of 0 but canopy closure of more than 10%. These cases were excluded, but did not appreciably affect the correlations.

Kalacska et al. (2005a,b) found a similar WAI (~0.4) to our estimate for late-successional tropical dry forest, but the contribution of WAI to the PAI in that forest was 14–23%, higher than the 11% that we found probably as a result of lower LAI estimates found in the tropical dry forest (1.7–5.7 LAI). Gower et al. (1999) reported WAI contributions to the PAI ranging from 5% to 35% for a variety of studies for coniferous and broadleaf forests. This wide range of WAI/PAI ratios suggests that the contribution of wood area to the LAI indirect estimates could be a result of the combined effect of the biome type and methodological approaches.

4.3. *Canopy vertical profiles*

Despite the lack of correlation among direct and indirect methods for forest floor measurements at the local scale, a result we had expected, we observed a strong similarity and good correlations between the direct-harvest LAI and the indirect methods along the vertical profiles. These correlations likely reflect the real increase in LAI with increasing depth in the canopy (distance from the top of the canopy to the forest floor), regardless of the size of the footprint or field of view. However, as cumulative direct-harvest LAI approached ~2 with increasing canopy depth, underestimation of the direct-harvest LAI by hemispherical photographs (GLA) increased, presumably more of an effect of an increase of the number of layers of leaves than an increase in leaf clumping. At shallow canopy depths, leaf clumping is expected to be high, potentially affecting the estimates of LAI by optical methods. However, a simultaneous decrease in the number of observable layers of leaves could compensate for the leaf clumping increase. The LAI-2000 performed better than hemispherical photographs with increasing canopy depth and LAI, showing no evidence of underestimation until LAI harvest was > 4 (Fig. 1).

4.4. *Canopy closure*

The relationships of indirect estimates of canopy closure with harvest LAI approach an asymptote as harvest LAI values go above 4–6 (Fig. 2), suggesting that in forests where the canopy closure approaches 80%, estimates of LAI are likely to be underestimated by canopy closure. The rate of change of the relationship between closure and harvest LAI for the LAI-2000 was lower than that of the GLA analysis, suggesting that at higher leaf areas the LAI-2000 would predict better direct-harvest LAI than the hemispherical photographs. The superior performance of the LAI-2000 is likely because radiation is processed as a continuous variable rather than as a threshold, as is done with the hemispherical photographs. Although the canopy closure calculations using the Beer–Lambert law for the LAI-2000 can be affected by inverted light gradients resulting from of openings between canopy layers and strong lateral light, the outcome is clear that at the relatively high LAI values in TRF optical sensors are approaching their limit to detect differences in LAI (Fig. 2).

Though the LAI 2000 showed better performance than the hemispherical photographs, one of the disadvantages of using the LAI-2000 is that it requires readings of incoming radiation above the canopy or in a clearing sufficiently large that vegetation does not obscure the field of view. This condition is difficult to attain in intact TRF, where the canopy is tall and large clearings within a suitable distance are unlikely. The use of a walk-up tower in the present study allowed access to the top of canopy so that simultaneous above- and below-canopy measurements could be made. The data here reflect the best possible circumstances for assessment of light conditions and canopy structure in TRF by the LAI-2000.

5. Conclusions

This study represents the first attempt to calibrate indirect assessments of LAI in TRF at the landscape level. These data should aid in the improvement of TRF primary production and water-balance models by providing information that can be used to improve estimates of LAI from indirect assessments made with the LAI-2000 and hemispherical photographs. In this study we found that the WAI is 0.67 and represents ~11% of the PAI calculated from direct harvesting. The LAI-2000 provided relatively accurate estimates of LAI, with 18% underestimation after correction for wood area. However, this instrument requires above-canopy or an open sky view for the reference sensor, a serious limitation beneath the closed and tall canopies of the TRF. Hemispherical photography analyzed with GLA had the highest underestimation of the direct-harvest LAI (38%) when only corrected for WAI. However, estimates of direct-harvest LAI significantly improved to 12–24% underestimation of direct-harvest LAI when corrected for leaf clumping. Hemispherical photographs analyzed using WinSCANOPY (only at the forest floor) yielded better results than those using GLA, with underestimation of 3 to 21%. For estimating vertical profiles of LAI, the indirect methods compared well to direct-harvest data at low direct-harvest LAI values. However, as the top-down cumulative direct-harvest LAI increases, estimates from both indirect methods get progressively worse. As the canopy closure and LAI increase, both optical methods show evidence of loss of sensitivity or inability to detect changes in LAI. For the characterization of light conditions within the forest canopy, indirect optical methods are useful tools. But for estimation of LAI, corrections for the effects of wood area and leaf clumping should be applied.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2013.04.010.

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