

Comparing direct and indirect methods of assessing canopy structure in a northern hardwood forest

Anne G. Rhoads, Steven P. Hamburg, Timothy J. Fahey, Thomas G. Siccama, and Richard Kobe

Abstract: Several methods exist for measuring forest canopies following disturbance, and the biases and differences among them are unclear. We compared techniques for measuring the northern hardwood forest's canopy structure at the Hubbard Brook Experimental Forest, New Hampshire, following the severe ice storm of January 5–10, 1998. Methods included leaf area index (LAI) using LI-COR's LAI-2000, visual damage assessments based on tree branch loss, radiation estimates from hemispherical photographs, and LAI determined from litterfall. LAI-2000 measurements were not significantly related to visual damage class estimates, but were strongly correlated with radiation estimates from hemispherical photographs and average LAI values from litterfall. LAI from the LAI-2000 and litterfall differed on a point-by-point basis, but were similar at the stand scale. The LAI-2000 has the highest precision for large-scale measurements. Visual damage estimates appear adequate for assessing large-scale patterns of disturbance intensity in the northern hardwood forest, but the LAI-2000 is more accurate at quantifying canopy structure at large plot or stand scales. Hemispherical photographs may also accomplish this, but are better suited to characterizing the distribution of canopy gaps and light availability patterns over time. Litterfall provides accurate and precise measurements of small-scale LAI patterns in deciduous forests and reveals species-specific patterns.

Résumé : Il existe plusieurs méthodes pour mesurer l'état du couvert forestier après une perturbation mais les biais et les différences propres à chacune de ces méthodes sont encore vagues. Nous avons comparé différentes techniques pour mesurer la structure du couvert de la forêt feuillue nordique à la Forêt Expérimentale d'Hubbard Brook au New Hampshire après l'importante tempête de verglas survenue du 5 au 10 janvier 1998. Les méthodes comprenaient la mesure de l'indice de surface foliaire (LAI) à l'aide du LAI-2000 de LI-COR, l'évaluation visuelle des dommages à partir des pertes de branches, l'estimation du rayonnement à l'aide de photographies hémisphériques et la détermination de LAI à partir de la chute de litière. La relation entre les mesures du LAI-2000 et les estimations visuelles de la classe de dommages n'était pas significative. Par contre, les mesures du LAI-2000 étaient fortement corrélées aux estimations du rayonnement à l'aide des photographies hémisphériques ainsi qu'aux valeurs moyennes de LAI déterminées à partir de la chute de litière. Les valeurs de LAI mesurées avec le LAI-2000 et celles obtenues à partir de la chute de litière différaient sur une base ponctuelle mais étaient similaires à l'échelle du peuplement. Le LAI-2000 a la plus grande précision pour les mesures à grande échelle. L'estimation visuelle semble adéquate pour évaluer les patrons à grande échelle de l'importance des dommages dans la forêt feuillue nordique mais le LAI-2000 est plus précis pour quantifier la structure du couvert à l'échelle des grandes places-échantillons ou des peuplements. Les photographies hémisphériques peuvent également satisfaire ce besoin mais sont mieux adaptées pour caractériser la distribution des trouées dans le couvert et l'évolution des patrons de disponibilité de la lumière dans le temps. La chute de litière fournit des mesures exactes et précises des patrons de LAI à petite échelle dans les forêts décidues et fait ressortir les patrons spécifiques à chaque espèce.

[Traduit par la Rédaction]

Received 9 April 2003. Accepted 15 September 2003. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 12 March 2004.

A.G. Rhoads.¹ Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, U.S.A.

S.P. Hamburg. Center for Environmental Studies, Brown University, Providence, RI 02912, U.S.A.

T.J. Fahey. Department of Natural Resources, Cornell University, Ithaca, NY 14853, U.S.A.

T.G. Siccama. School of Forestry and Environmental Studies, Yale University, New Haven, CT 06520, U.S.A.

R. Kobe. Michigan State University, East Lansing, MI 48824, U.S.A.

¹Corresponding author (Anne_Rhoads@brown.edu).

Introduction

The ability to measure forest canopy structure quickly and accurately is critical to understanding the response of forests to disturbance on several scales, from the individual tree to the community and the ecosystem. Changes in a tree's canopy alter rates of photosynthesis and evapotranspiration and hence net ecosystem productivity (Chason et al. 1991). Disturbances that lead to the creation of forest canopy gaps can change competitive interactions by making light, moisture, nutrients, and space available to survivors and new recruits (Oliver and Larson 1996). This in turn can determine the architecture of individual trees (Zimmerman and Brown 1971; Oliver and Larson 1996), regeneration of woody and herbaceous plants (Canham et al. 1994; Kobe et al. 1995), and nutrient cycling through the ecosystem (Vitousek 1985; Houlton et al. 2003).

Because the accuracy, precision, and advantages of different methods of measuring forest canopies have not been thoroughly quantified, it is difficult to compare the effects of varying disturbances across studies and diverse landscapes. Many reports assessing canopy closure following disturbance have relied on visual canopy assessments (Whitney and Johnson 1984; Seischab et al. 1993). This technique, while relatively fast, is subjective and imprecise. The most widely used quantitative metric of canopy structure is leaf area index (LAI) (Waring 1985; Cutini et al. 1998), which has proven useful in measuring the impacts of natural and anthropogenic disturbances on forest ecosystems. The direct determination of LAI may involve destructive sampling of the canopy (Gower and Norman 1991; Jurik et al. 1985), the use of litterfall traps (Jurik et al. 1985), and the measurement of LAI by tabletop leaf area meters (Foster 1988; Kull et al. 1999). Several studies have determined leaf area directly by determining a leaf area : dry mass ratio of leaf samples (Jurik et al. 1985; Kull et al. 1999), but this technique is time consuming, may be limited by a poorly defined sampling area, and may not produce accurate or unbiased results (Jurik et al. 1985; Cutini et al. 1998).

Indirect methods for evaluating LAI are gaining in popularity because they provide nondestructive, rapid measures of defined areas (Norman and Campbell 1989; Chason et al. 1991). Hemispherical photographs have been used to determine incident radiation through measurements of gap size (Rich 1990; Whitmore et al. 1993). The photos do not accurately measure photon flux density in closed canopies. Some studies have found the technique to be effective at assessing relative differences in light availability and distribution (Nicotra et al. 1999), but others have demonstrated that hemispherical photographs fail to detect these differences in low light conditions (Machado and Reich 1999). The greatest strength of hemispherical photographs may be their utility in understanding canopy structure and gap distribution (Nicotra et al. 1999). Photographic analysis, though, is laborious (Nicotra et al. 1999) and requires a great deal of effort to maintain a high level of precision.

Alternatively, LAI can also be indirectly measured using the LI-COR LAI-2000 plant canopy analyzer (LI-COR Incorporated, Lincoln, Nebr., U.S.A.). Surprisingly, few studies have tested the accuracy and precision of the LAI-2000

in temperate forests, and most comparisons that do exist took place in coniferous stands (Gower and Norman 1991; Deblonde et al. 1994). Accurate measurements with the LAI-2000 require diffuse light conditions to avoid excessive reflection off leaves, so measurements must be taken at dawn, dusk, or on uniformly overcast days. Readings must also be taken simultaneously in the forest and in a large clearing to provide background correction. The LAI-2000 has been found to provide reliable, relative measures of canopy cover in tropical wet forest settings, correlating with percent diffuse light transmittance as measured by a quantum sensor (Nicotra et al. 1999). Some studies have found absolute LAI values obtained with the LAI-2000 to be correlated with but lower than LAI measured with litterfall collectors (Deblonde et al. 1994; Cutini et al. 1998). For example, Cutini et al. (1998) found LAI values from the LAI-2000 to be 12% lower than those obtained through litterfall; this underestimation was ascribed to overlapping leaves, gaps in the canopy, or light at the horizon. One study found the LAI-2000 to produce a stronger relationship with instantaneous photon flux density than other rapid estimates, including hemispherical photographs and photodiodes measuring instantaneous percent photosynthetic photon flux density (Machado and Reich 1999).

Very little work has been done to compare multiple measures of forest canopy cover following disturbance events in temperate deciduous forests. A comparison of more techniques, at more sites, and in more forest types is required to determine the efficacy of different measures of canopy cover. This study compared estimates of canopy cover in a northern hardwood forest following an intense ice storm using the LI-COR LAI-2000, visual damage class assessments, hemispherical photographs, and litterfall traps. The goal of the study was to compare the different measures and assess the suitability of using a single method across sites and disturbance intensities. Measurements were made following an ice storm that heavily impacted the forests of the northeastern United States and southeastern Canada (Irland 1998; Rhoads et al. 2002).

Materials and methods

Study site

Hubbard Brook Experimental Forest (HBEF), located in Woodstock, New Hampshire (43°56'N, 71°45'W), encompasses 3160 ha of the White Mountain National Forest. The climate of the region is cool, temperate, humid continental. The average temperature in January is -9 °C and in July is 19 °C, and the forest receives an average of 123 cm of precipitation per year, one-third to one-quarter of which falls as snow. The bedrock of the area is Rangely formation and is overlain with unsorted basal till. Till depths range from 0 to 3 m and tend to increase at lower elevations (T.G. Siccama, unpublished data). The soils are primarily well-drained Spodosols (coarse, loamy, mixed, frigid, Typic Haplorthods) with sandy loam to loamy sand textures (Johnson 1989).

The HBEF is a northern hardwood forest, with the highest elevations characterized as a subalpine spruce – fir forest. Prior to 1900, the midelevation forests of the region were described as spruce–hardwoods (Chittenden 1904; Braun

1950), with logging and agricultural disturbance shifting species composition. The HBEF watershed was cleared of most merchantable trees from 1880 to 1917. The hurricane of 1938 further affected the forest, with some areas experiencing high levels of damage (Peart et al. 1992). The stands of mature forest are now dominated by beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula alleghaniensis* Britt.), with spruce (*Picea rubens* Sarg.) and fir (*Abies balsamea* (L.) Mill.) primarily found on ridges and rocky areas (Bormann et al. 1970).

The study took place on the south-facing watersheds 6 (WS 6) and 1 (WS 1) at the HBEF, both of which are subdivided into 25 m × 25 m permanent plots. WS 6 is the biogeochemical reference watershed covering 13.2 ha, from 549 to 792 m elevation. In 1999, WS 1 (11.8 ha; 488–747 m elevation) was treated with 4.3 Mg/ha of CaSiO₃ (wollastonite). At the time of the January 5–10, 1998, ice storm, sugar maple, beech, and yellow birch dominated WS 1 and WS 6 on both a basal area and density basis (Rhoads et al. 2002).

Visual canopy assessment

Prior to leaf out in May 1998, all trees 20 cm diameter at breast height (DBH) in alternating rows of plots within the ice damage zone were tagged (above 560 and 624 m on WS 1 and WS 6, respectively), diameters (DBH in cm) measured, and a damage rank assigned based on the percentage of broken branches (0% damage = 0, 1%–25% = 1, 26%–50% = 2, 51%–75% = 3, 76%–100% = 4, crown gone = 5, uprooted or broken off at base = 6). Weighted mean damage class was determined for each 25 m × 25 m plot using the basal area of each tree as a weighting factor. The loss of leaf area was estimated for each damaged tree and plot by applying visual damage class estimates to allometric relationships for the HBEF (Whittaker et al. 1974; Siccama et al. 1994).

Indirect light measurements

The LI-COR LAI-2000 plant canopy analyzer was used to measure canopy light interception at five different zenith angles (7°, 23°, 38°, 53°, and 68°), with the gap fraction calculated for each ring using the ratio of above- and below-canopy measurements (Welles 1990; Welles and Norman 1991). We used two LAI-2000 sensors: one carried to sampling points under the canopy (below canopy) of each watershed and one placed in a large (approximately 20 ha), level clearing 2.5 km away (above canopy). The above canopy sensor was programmed to take readings every 15 s. Readings from the below- and above-canopy sites were within 0–6 s of each other. Above- and below-canopy readings were combined and LAI calculated as a function of gap fraction using LI-COR's C2000 software (Welles and Norman 1991).

LAI-2000 readings were taken at 22 plots selected from middle and upper elevation areas impacted by the ice storm on WS 1 (10 plots) and WS 6 (12 plots) using a stratified random design. The plots were first stratified by damage class (0 to <1, 1 to <2, and 2 to <3), and a subset was then selected from each damage category proportional to their distribution within each elevation zone to be used in LAI-2000 sampling. No ice damage occurred below 560 m on

WS 1 and below 624 m on WS 6. Five plots were randomly selected from each of these areas to serve as undamaged references.

Within the center of the 32 plots selected for LAI-2000 measurements, a 15 m × 15 m subplot was delineated to minimize the influence of the forest canopy from adjoining plots. Ten points were randomly chosen within each of these subplots. In July of 1998, one LAI measurement (sensor held at 0°) was taken at each of these points above the shrub stratum (2.5 m above the ground). Each measurement included three readings that were later averaged. Readings were taken at dawn and dusk to meet the diffuse light and uniform sky requirements of the LAI-2000. These periods were defined as the times before sunrise and after sunset when no beam radiation reflected off canopy leaves, but light was sufficient for maneuvering in the forest. Only the readings of the three inner rings of the optical sensor were used to eliminate the influence of trees outside the plots (from 0° to 43° of zenith). The sensor's field of view was a circle with a radius of less than 20 m and an area of less than 1300 m², assuming a canopy height of 22 m (T.G. Siccama, unpublished data). The true value is likely less than this calculated value because of the dense nature of the forest.

LAI-2000 readings were also taken in 12 plots adjacent to the western border of WS 6 at HBEF where hemispherical photographs had been taken in 1998. The permanent plots, established in 1995, measure 45 m × 45 m with a 25 m × 25 m interior and a 10-m buffer on all sides. Hemispherical photos and LAI-2000 readings were taken in 1.2 m × 1.2 m permanent subplots at four to six randomly determined points within each plot. In this analysis, all five rings of the LAI-2000's optical sensor were used because this 148° view is the closest to the 180° image captured in the hemispherical photographs. In this comparison, the LAI-2000 measured LAI (m²/m²) and diffuse noninterceptance (DIFN), a measure of diffuse light transmittance.

Hemispherical photographs were taken using a Nikon N70 camera with a Sigma Fisheye 180° lens. The tripod-mounted camera was oriented towards true north and leveled before 180° images of the canopy were captured on Ektachrome 400 color slide film. Slides were scanned with a Polaroid Quick Scan slide scanner and digitized images were analyzed with GLA software (Frazer et al. 1999) to compute percent transmittance of diffuse and direct beam photosynthetically active radiation. The software calculates percent transmittance by imposing latitude-specific daily solar tracks on the canopy hemisphere and summing photosynthetically active radiation that penetrates small gaps in the canopy over the growing season, which we specified as 15 May – 15 September.

Litterfall measurements

Litterfall measurements were made within 1.0-ha plots at three elevations (525, 570, and 774 m) in the forest immediately west of WS 6. Leaf litterfall was collected using random arrays of twelve 0.10-m² rectangular collectors lined with 1-mm mesh nylon screening and anchored with 4-cm PVC pipe. Litter was collected in June, August, and November. The leaf litter from each collector was sorted by species,

and the number of leaves of each species was counted. The leaf litter samples of each species were pooled by site, and a random subsample of 20 leaves was used to estimate the average area per leaf. The subsamples were flattened in a plant press, photocopied onto acetate, and the area measured to $\pm 0.1 \text{ cm}^2$ using a LI-COR leaf area analyzer. LAI was estimated for each litterfall collector by multiplying the average leaf area for a species by the number of leaves summed across all species and divided by the area of the collector.

LAI-2000 measurements were taken above each litter trap in late July 1999. A technical problem with the third ring of the below-canopy LAI-2000 affected half of the data in this comparison. As a result, the third and fifth rings of the optical sensor were masked when calculating LAI. The data collected on the day when ring 3 was functional was further examined to check the appropriateness of the assumption that masking rings 3 and 5 would not jeopardize the data. On average, LAI values calculated with rings 3 and 5 masked were 5% lower than those calculated with rings 4 and 5 masked, but this difference was not significant ($t = -1.3$, $p = 0.2$). Masking rings 3 and 5 did not bias the data in a way that systematically increased or decreased values, validating our decision. By masking the third and fifth rings, the field of view of the sensor was a circle with a radius of less than 35 m and an area of less than 3800 m².

Data analysis

Average coefficients of variation within plots were determined to evaluate the variation in the different measures. This calculation could not be made for visual damage class estimates, since only one estimate was made in each plot. Comparisons between damage class and LAI-2000 measurements were performed using ordinal logistic regression, with LAI predicting damage class after weighting damage class by basal area. The relationships between LAI-2000 measurements and radiation estimates from hemispherical photographs were examined with simple linear regression using LAI to predict beam, diffuse, and global radiation. DIFN measured by the LAI-2000 was also compared with diffuse radiation estimated with hemispherical photographs using simple regression. This test was also used to compare LAI-2000 and litterfall trap estimates of LAI, with LAI-2000 readings at each trap predicting litterfall trap measurements. LAI values obtained using litterfall traps and the LAI-2000 were also compared using ANOVA with method (litterfall trap or LAI-2000) nested within elevation to predict LAI values. All analyses used JMP 3 (SAS Institute Inc. 1995).

Results and discussion

LAI-2000 values were less variable within plots than radiation estimates from hemispherical photographs: 37% less than global, 43% less than beam, 23% less than diffuse radiation. Variation in LAI values within plots was similar for the LAI-2000 and litterfall traps (14% and 17%, respectively; Table 1), illustrating the precision of these two methods. To determine if the greater precision of the data also reflects increased accuracy, one must examine how the actual measurements compare among techniques.

Table 1. Average coefficient of variation (C.V.) within plots of different methods used to measure canopy cover.

Methods compared	C.V.
LAI-2000 and litterfall traps	
LAI from LAI-2000	15
Global radiation from hemispherical photographs	42
Beam radiation from hemispherical photographs	58
Diffuse radiation from hemispherical photographs	38
LAI-2000 and hemispherical photographs	
LAI from LAI-2000	14
LAI from direct measure of litterfall	17

Note: Data collected at Hubbard Brook Experimental Forest, N.H., U.S.A. LAI, leaf area index.

Although LAI tended to be lower in plots with higher weighted visual damage class, ordinal logistic regression revealed no significant relationship for the damaged plots of WS 1 and WS 6 at HBEF ($\chi^2 = 2.45$, $p = 0.12$). Branch loss from the visual assessment was also used to estimate leaf biomass lost during the storm based on allometric regressions (Whittaker et al. 1974; Siccama et al. 1994), but this did not increase the strength of the relationship between visual damage class and LAI. The ordinal nature of damage assessments, in contrast with the continuous data from the LAI-2000 and combined with the subjective nature of assigning damage class values, is most likely responsible for the higher variation in visual damage estimates. The LAI-2000 may have also overestimated the LAI of ice-damaged trees with bare branches (Gower and Norman 1991). In healthy trees, branch surfaces compose only a small proportion of canopy surface area. However, LAI loss resulting from heavy ice damage increases the contribution of branches to total LAI. This suggests that in plots assigned high damage class values (and thus with intense leaf loss), the raw LAI-2000 values may be somewhat skewed, and corrections based on stem surface area may be needed. We also investigated the possibility that the LAI-2000 overestimated LAI in plots with high densities of small diameter (2–8 cm DBH) beech sprouts that tend to dominate the understory above 600 m at the HBEF. If these sprouts were in close proximity to the LAI-2000 sensor, LAI might have been inflated. We found no evidence to support this hypothesis. Simple regression analysis found no effect of beech sprout density on LAI in plots undamaged by the ice storm ($y = 0.03x + 4.9$, $r^2 = -0.11$, $p = 0.79$). In damaged plots, we found that LAI decreased with increasing beech density ($y = -0.09x + 4.8$, $r^2 = 0.21$, $p = 0.02$). This likely reflects a highly damaged beech overstory. Beech was the species most severely damaged by the ice storm (Rhoads et al. 2002). The LAI-2000, therefore, appears to be revealing true LAI patterns.

The weak relationship between LAI-2000 and visual damage class may also reflect the differences in the effective sampling area of the two techniques. Although measurements were based within the same 25 m \times 25 m plots, the visual assessments were made only on trees within the plot boundaries, while the LAI-2000 probably captured data from roughly twice the area of the plot.

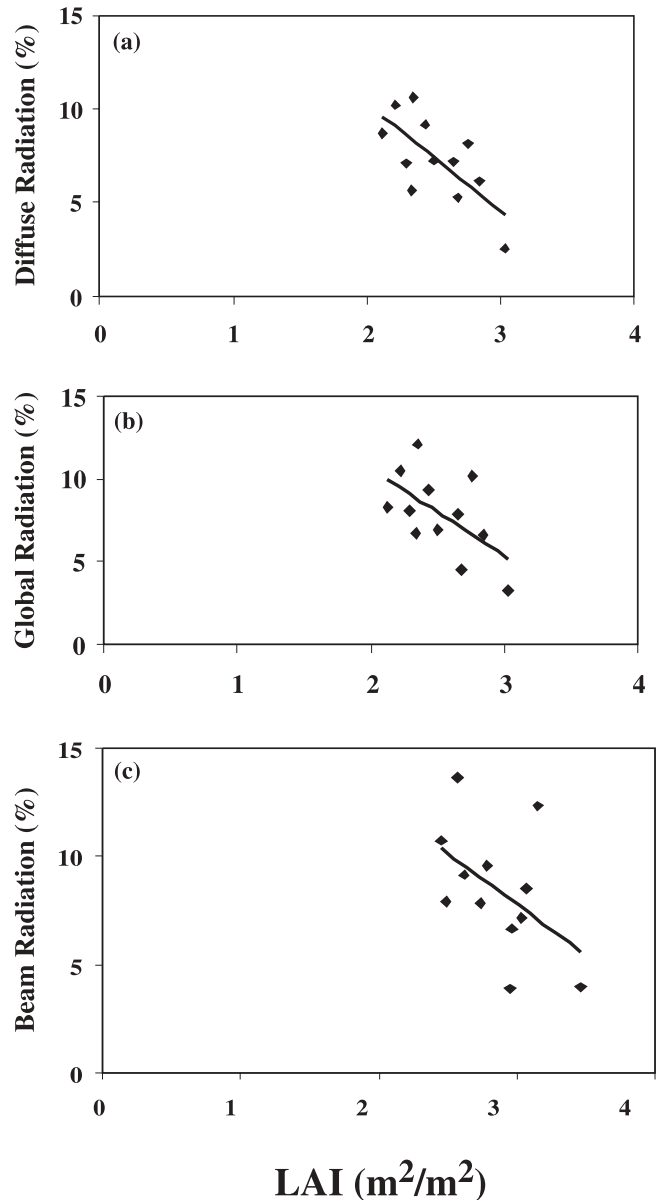
Other authors have shown that LAI is more strongly related to photosynthetic photon flux density than hemispherical photographs (Machado and Reich 1999). In our study, the ability of the LAI-2000 to measure canopy damage through relative light availability was evident in the comparison between LAI-2000 readings and radiation estimates using hemispherical photographs. A significant relationship was found when using LAI as measured by the LAI-2000 to predict both diffuse ($r^2 = 0.48$, $p = 0.012$) and global ($r^2 = 0.33$, $p = 0.05$) radiation (Fig. 1a, 1b). A much weaker relationship existed when using LAI to predict beam radiation ($r^2 = 0.20$, $p = 0.15$) (Fig. 1c). Our finding of a less significant relationship between LAI and global radiation as compared with LAI and diffuse radiation makes sense given that unlike the global estimate, the LAI-2000 does not take solar tracks into account (e.g., the fact that the north side of a gap receives more light than the south side in the Northern Hemisphere) (Chazdon and Field 1987). Thus, diffuse values calculated from canopy photos are closest to those that the LAI-2000 measures. DIFN as measured by the LAI-2000 has been found to be an unbiased estimate of fractional transmittance (Machado and Reich 1999). We found a slightly stronger relationship between DIFN and diffuse radiation from hemispherical photographs than between LAI and diffuse radiation ($r^2 = 0.50$, $p = 0.0098$) (Fig. 2).

The higher variability in each of the radiation estimates as compared with LAI measured by the LAI-2000 may reflect that analysis of photographs is somewhat subjective. An alternative explanation is that the hemispherical photos are more sensitive to capturing fine-scale variation within plots.

Estimates of LAI were very similar for the LAI-2000 and litter traps in three deciduous forest plots at the HBEF ($F = 0.75$, $p = 0.53$) (Fig. 3). In the 525-m and 774-m plots, the stand-level LAI estimates were nearly identical, while in the 570-m plot the litterfall method gave a 14% higher estimate than the LAI-2000. The average difference between measurements from these two methods in our three study plots is much smaller than that observed by Cutini et al. (1998) in an Italian deciduous forest. Comparisons between these methods on a point-by-point basis revealed no significant relationships, a finding that is not surprising given the large sampling area of the LAI-2000. Hence, at smaller spatial scales, the litter trap is more appropriate for measuring forest LAI than the LAI-2000, but given that leaves do not fall straight down, it is hard to know the effective sampling area of the litter traps.

The efficiency of the litterfall traps is unknown, but the consistency of year-to-year LAI estimates suggests that the method probably provides accurate estimates. Across 5 years of collection before the ice storm, the coefficient of variation in the mean estimated LAI between years for the three plots averaged 6%. Another study found litterfall traps to consistently overestimate LAI when compared with direct LAI measurement through harvesting (Jurik et al. 1985). The precision of the litterfall method for estimating LAI probably depends primarily upon the collection area of the traps. The 0.1-m² traps employed in this study resulted in within-plot coefficients of variation ranging from 14% to 18% for the different plots, averaged across 8 years of collection. Another source of error in the litterfall method is sampling error in the estimation of area per leaf. Considerable within-

Fig. 1. Simple regression analysis using LAI (leaf area index) (m^2/m^2) values measured using a LI-COR LAI-2000 to predict percentage of total solar radiation estimated by hemispherical photographs for (a) diffuse radiation (% total transmittance) ($y = -5.71x + 21.712$, $r^2 = 0.48$, $p = 0.012$), (b) global radiation (% total transmittance) ($y = -5.23x + 21.062$, $r^2 = 0.33$, $p = 0.05$), and (c) beam radiation (% total transmittance) ($y = -4.74x + 20.372$, $r^2 = 0.20$, $p = 0.15$). The data were collected in July 1998, the first growing season following the January 1998 ice storm, from 12 plots in the northern hardwood forest west of watershed 6 of the Hubbard Brook Experimental Forest, N.H., U.S.A.



species variation was observed in area per leaf both among years and among plots, with the average coefficient of variation across all species and plots over the years of measurement being 18%.

Our results point to the desirability of using different measures of canopy cover depending on the question being

Fig. 2. Simple linear regression using average diffuse noninterceptance (DIFN) values measured with LI-COR LAI-2000 to predict estimates of diffuse radiation (% total transmittance) measured with hemispherical photographs ($y = 39.8x + 1.3097$, $r^2 = 0.50$, $p = 0.0098$). Data were collected from west of watershed 6 of the Hubbard Brook Experimental Forest, N.H., U.S.A.

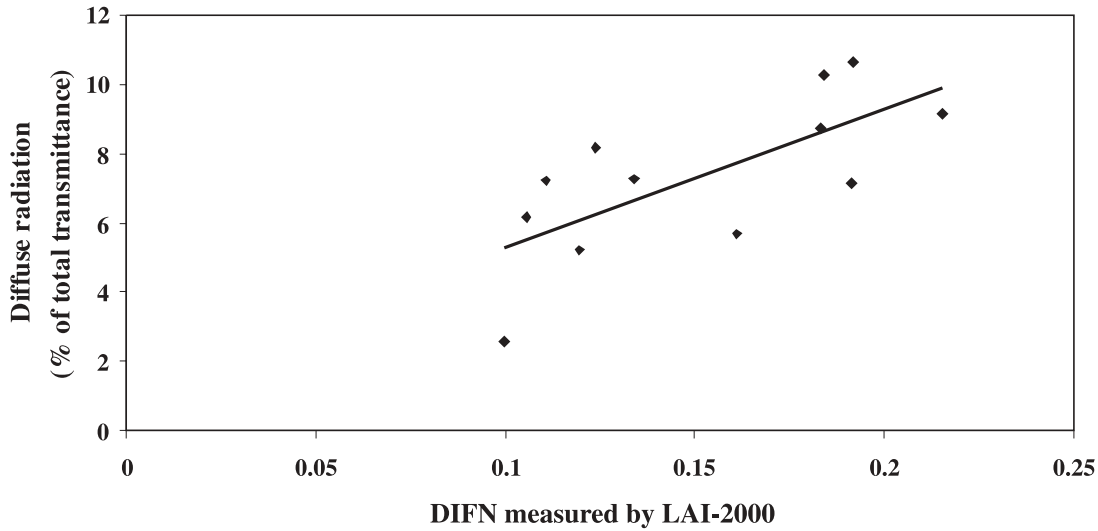
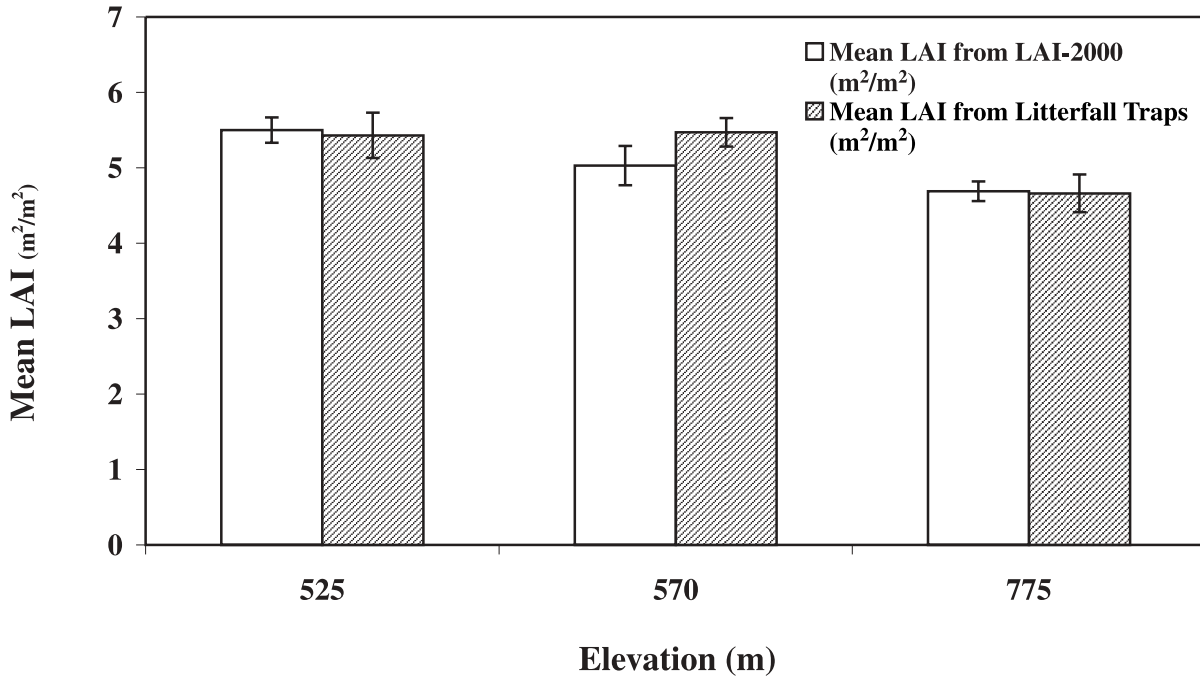


Fig. 3. Mean leaf area index (LAI) values within each elevation zone (525, 570, and 774 m) measured using a LI-COR LAI-2000 and litterfall traps (with standard error bars). Data were collected west of watershed 6 at the Hubbard Brook Experimental Forest, N.H., U.S.A.



asked. Though somewhat subjective, visual damage assessments are effective measures of landscape-level disturbance intensity during the dormant season when the other three methods cannot be used. Visual assessments have been found to be accurate enough to predict disturbance-caused ecosystem changes such as nitrate flux in stream water (Houlton et al. 2003). For a quantitative measure of canopy disturbance at a large plot or forest stand scale, the LAI-2000 appears to provide an accurate and precise measure. Variation among data is low and measures are similar to

those obtained from hemispherical photographs and direct LAI from litterfall baskets averaged across larger areas. The accuracy of the LAI-2000 may be lower in highly damaged canopies where significant areas of branches lack leaf cover, and in these situations background corrections during the leafless period may be necessary. The requirements for effectively using the LAI-2000 include the need for diffuse light conditions, no precipitation, and a large clearing or tower in which to take above-canopy readings, creating significant logistical demands. However, since LAI-2000 mea-

surements can be made quickly using only a single visit to a site and data analysis is relatively easy, the LAI-2000 represents the fastest accurate method for measuring LAI in temperate forests. The ease with which canopy cover can be measured is becoming increasingly important, as the spatial scale of studies is increasing from the stand to landscape level (Gower and Norman 1991). The LAI-2000 has also been found effective at measuring changes in canopy structure over time following a disturbance (Rhoads et al. 2002) and at quantifying the vertical distribution of foliage (Fahey et al. 1998).

Hemispherical photographs provide an accurate measure of larger scale canopy structure dynamics, yielding similar results to the LAI-2000, but with lower precision and greater effort. However, hemispherical photographs are effective if the goal is the characterization of canopy structure and distribution of gaps. Hemispherical photographs may also be more appropriate for predicting changes in light conditions throughout the year as compared with light sensors like quantum sensors or the LAI-2000 (Nicotra et al. 1999).

Litterfall traps are the most effective approach to quantifying LAI on smaller plots in deciduous forests, and precision is relatively high when used for this purpose. This is also the only method that can provide species-specific LAI values, but it is the most labor-intensive of the approaches we compared.

Overall, the LAI-2000, hemispherical photographs, and leaf-litter traps all provided accurate measures of forest canopy differences within the northern hardwood forest being studied, with the LAI-2000 having the greatest precision. Each of the three methods provides different information, and each is an effective approach depending on the question being asked. The LAI-2000 is an effective approach on the landscape scale, while hemispherical photographs are appropriate when detailed light data is needed. Litterfall traps are required for obtaining species-level data. When assessing the effects of a disturbance on forest canopies, visual damage surveys are the easiest to carry out, but with their lower accuracy they should be used when dormant season data is required or large-scale relative indices are sufficient.

Acknowledgements

We greatly appreciate field and technical assistance provided by Theresa Mann, Geoff Wilson, and Cindy Wood. This project was funded through HBEF Long Term Ecological Research (LTER) funding and a Small Grants for Exploratory Research (SGER) grant to Gene Likens from the National Science Foundation (DEB-9810221). This research was conducted at the Hubbard Brook Experimental Forest, which is owned and operated by the Northeastern Research Station, USDA Forest Service, Newtown Square, Pa. This is a contribution to the Hubbard Brook Ecosystem Study.

References

- Bormann, F.H., Siccama, T.G., Likens, G.E., and Whittaker, R.H. 1970. The Hubbard Brook Ecosystem Study: composition and dynamics of the tree stratum. *Ecol. Monogr.* 40: 377–388.
- Braun, E.L. 1950. *Deciduous forests of eastern North America*. The Blakiston Co., Philadelphia.
- Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests — interspecific variation in light transmission by canopy trees. *Can. J. For. Res.* 24: 337–349.
- Chason, J.W., Baldocchi, D.D., and Huston, M.A. 1991. A comparison of direct and indirect methods for estimating forest canopy leaf area. *Agric. For. Meteorol.* 57: 107–128.
- Chazdon, R.L., and Field, C.B. 1987. Photographic estimation of photosynthetically active radiation: evaluation of a computerized technique. *Oecologia*, 73: 525–532.
- Chittenden, A.K. 1904. Forest conditions of northern New Hampshire. *In* State of New Hampshire biennial report of the forestry commission 1903–1904. Concord, N.H.
- Cutini, A., Matteucci, G., and Scarascia, G.S. 1998. Estimation of leaf area index with the Li-COR LAI-2000 in deciduous forests. *For. Ecol. Manage.* 105: 55–65.
- Deblonde, G., Penner, M., and Royer, A. 1994. Measuring leaf area index with the LI-COR LAI-2000 in pine stands. *Ecology*, 75: 1507–1511.
- Fahey, T.J., Battles, J.J., and Wilson, G.F. 1998. Response of early successional northern hardwood forests to changes in nutrient availability. *Ecol. Monogr.* 68: 183–212.
- Foster, J.R. 1988. The potential role of rime ice defoliation in tree mortality of wave-regenerated balsam fir forests. *J. Ecol.* 76: 172–180.
- Frazer, G.W., Canham, C.D., and Lertzman, K.P. 1999. Gap light analyzer (GLA): imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, B.C., and the Institute of Ecosystem Studies, Millbrook, N.Y.
- Gower, S.T., and Norman, J.M. 1991. Rapid estimation of leaf area index in conifer and broad-leaf plantations. *Ecology*, 72: 1896–1900.
- Houlton, B.Z., Driscoll, C.T., Fahey, T.J., Groffman, P.M., and Likens, G.E. 2003. Nitrogen dynamics in ice storm-damaged forest ecosystems: implications for nitrogen limitation theory. *Ecosystems*, 6: 431–443.
- Irland, L.C. 1998. Ice storm 1998 and the forests of the northeast. *J. For.* 96: 32–40.
- Johnson, C.E. 1989. The chemical and physical properties of a northern hardwood forest soil: harvesting effects, soil–tree relations, and sample size determination. Ph.D. thesis, University of Pennsylvania, Philadelphia.
- Jurik, T.W., Briggs, G.M., and Gates, D.M. 1985. A comparison of four methods for determining leaf area index in successional hardwood forests. *Can. J. For. Res.* 15: 1154–1158.
- Kobe, R.K., Pacala, S.W., Silander, J.A., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5: 517–532.
- Kull, O., Broadmeadow, M., Kruijt, B., and Meir, P. 1999. Light distribution and foliage structure in an oak canopy. *Trees*, 14: 55–64.
- Machado, J.L., and Reich, P.B. 1999. Evaluation of several measures of canopy openness as predictors of photosynthetic photon flux density in deeply shaded conifer-dominated forest understory. *Can. J. For. Res.* 29: 1438–1444.
- Nicotra, A.B., Chazdon, R.L., and Iriarte, S.V.B. 1999. Heterogeneity of light and woody seedling regeneration in tropical wet forests. *Oecologia*, 80: 1908–1926.
- Norman, J.M., and Campbell, G.S. 1989. Canopy structure. *In* Plant physiological ecology; field methods and instrumentation. Edited by R.W. Pearcy, J. Ehleringer, H.A. Mooney, and P.W. Rundel. Chapman & Hall Inc., New York. pp. 301–325.

- Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley & Sons Inc., New York.
- Peart, D.R., Cogbill, C.V., and Palmiotto, P.A. 1992. Effects of logging history and hurricane damage on canopy structure in a northern hardwood forest. *Bull. Torrey Bot. Club*, **119**: 29–38.
- Rich, P.M. 1990. Characterizing plant canopies with hemispherical photographs. *Remote Sensing Reviews*, **5**: 13–29.
- Rhoads, A.G., Hamburg, S.P., Fahey, T.J., Siccama, T.G., Hane, E.N., Battles, J., Cogbill, C., Randall, J., and Wilson, G. 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. *Can. J. For. Res.* **32**: 1763–1775.
- SAS Institute Inc. 1995. JMP 3.2. SAS Institute Inc., Cary, N.C.
- Seischab, F.K., Bernard, J.M., and Eberle, M.D. 1993. Glaze storm damage to western New York forest communities. *Bull. Torrey Bot. Club*, **120**: 64–72.
- Siccama, T.G., Hamburg, S.P., Arthur, M.A., Yanai, R.D., Bormann, F.H., and Likens, G.E. 1994. Corrections to allometric equations and plant tissue chemistry for Hubbard Brook Experimental Forest. *Ecology*, **75**: 246–248.
- Vitousek, P.M. 1985. Community turnover and ecosystem nutrient dynamics. *In* The ecology of natural disturbance and patch dynamics. *Edited by* S.A. Pickett and P.S. White. Academic Press Inc., New York. pp. 325–333.
- Waring, R.H. 1985. Imbalanced forest ecosystems: assessments and consequences. *For. Ecol. Manage.* **12**: 93–112.
- Welles, J.M. 1990. Some indirect methods of estimating canopy structure. *Remote Sensing Reviews*, **5**: 31–43.
- Welles, J.M., and Norman, J.M. 1991. Instrument for indirect measurement of canopy architecture. *Agron. J.* **83**: 818–825.
- Whitmore, T.C., Brown, N.D., Swaine, M.D., Kennedy, D., Goodwinbailey, C.I., and Gong, W.K. 1993. Use of hemispherical photographs in forest ecology — measurement of gap size and radiation totals in a Bornean tropical rain forest. *J. Trop. Ecol.* **9**: 131–151.
- Whittaker, R.H., Bormann, F.H., Likens, G.E., and Siccama, T.G. 1974. The Hubbard Brook Ecosystem Study: forest biomass and production. *Ecol. Monogr.* **44**: 233–252.
- Whitney, H.E., and Johnson, W.C. 1984. Ice storms and forest succession in southwestern Virginia. *Bull. Torrey Bot. Club*, **111**: 429–437.
- Zimmerman, M.H., and Brown, C.L. 1971. Trees structure and function. Springer-Verlag New York Inc., New York.