A comparison of direct and indirect methods for estimating forest canopy leaf area

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ABSTRACT

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Two indirect gap fraction methods for estimating leaf area index (LAI) are compared with estimates from litterfall collections in a mixed-age oak–hickory forest. One indirect method uses averaged, direct beam penetration data obtained with a moving tram. The second uses a portable light sensor system that measures diffuse light penetration for five sky sectors between zenith angles 0 and 75°. Data were collected from September 1989 to January 1990.

The Poisson model and the negative binomial model of gap frequency were applied to estimate LAI from observed transmittances. With the Poisson model, an assumption of a random leaf spatial distribution contributes to an underestimation of LAI by as much as 45%; this is because leaves at this site are actually clumped at both large and small scales. The negative binomial, which requires determination of a clumping parameter, produces estimates comparable with those of the litterfall method.

Both indirect techniques accurately describe temporal changes in leaf area using either the Poisson or negative binomial model. The portable system also allows easy estimation of the spatial variation in leaf area within the site or between sites, and it can be used to obtain a vertical profile of leaf area.

INTRODUCTION

Forest canopy structure is a complex and dynamic outcome of the evolutionary and ecological interactions and feedbacks between vegetation and environment. As such, canopy structure is a key feature of any forest ecosystem which both influences and is influenced by numerous ecosystem processes (Campbell and Norman, 1989; Norman and Campbell, 1989). For instance, canopy structure strongly affects the net primary productivity of the entire ecosystem and regulates the light, temperature, wind, and moisture environments of the subcanopy and forest floor (Meyers and Paw U, 1986, 1987). Thus, understanding and quantifying canopy characteristics is critical in modeling these processes and in predicting ecosystem responses.

One of the most important characteristics of canopy structure is leaf area index (LAI), the total one-sided foliage area per unit soil surface area. Knowledge of cumulative LAI is critical for the estimation of a number of important ecosystem processes, including CO_2 flux, evapotranspiration, rainfall interception, and dry deposition. Information on the vertical distribution of leaf area is essential to such analyses as biogenic source–sink strengths of trace gas within the canopy, modeling penumbra, and modeling drag and work by the foliage on wind (Meyers and Paw U, 1987). Numerous direct and indirect methods for estimating LAI have been used with varying degrees of success (Ross, 1981; Campbell and Norman, 1989; Norman and Campbell, 1989; Welles, 1990).

Direct techniques for estimating LAI include the point quadrat method (Warren Wilson and Reeve, 1960), the stratified-clip method (Hutchison et al., 1986), the dispersed individual plant method (Norman and Campbell, 1989), and the litterfall collection method (Harris et al., 1973; Grizzard et al., 1976; Neumann et al., 1989). Leaf sampling methods are extremely labor intensive and require many replicates to reduce sampling errors. The litterfall technique is simpler but depends on the assumption that the collectors obtain a random sample of the overlying leaves that fall. This method is more successful in deciduous forests that have a single leaf-fall season than in evergreen forests that have more continuous leaf loss and replacement.

There are a number of indirect approaches that relate total leaf area to the radiation environment below the canopy through inversion of an appropriate radiative transfer model (Ross, 1981; Norman and Campbell, 1989). For instance, gap fraction methods relate leaf area to the probability of light passing unintercepted through the plant canopy (Lang et al., 1985; Lang and Xiang, 1986; Perry et al., 1988). This probability of light penetration, or the gap fraction, is a function of the cumulative foliage area, the angular distribution of foliage elements, and the angle of incoming sunlight.

A number of simplifying assumptions are usually made about canopy architecture to model light penetration and to assess canopy leaf area. The canopy is often modeled as a series of one-dimensional layers that are horizontally homogeneous. Foliage elements may be assumed to have a given angular distribution and are usually assumed to be randomly distributed azimuthally and in space (Nilson, 1971; Lang et al., 1985; Perry et al., 1988; Campbell and Norman, 1989; Neumann et al., 1989). Foliage elements are also considered to be optically black; thus scattering or transmission of light is assumed to be inconsequential.

This study evaluates two indirect methods for estimating leaf area by comparing the indirect estimates with direct estimates derived from litterfall. One indirect method is based on the penetration of direct beam sunlight measured at different zenith angles (degrees from vertical) over the course of a day. The second uses the Li-Cor model LAI-2000 Plant Canopy Analyzer, (Li-

Cor, Lincoln, NE) which measures diffuse light penetration from several different zeniths or sky sectors simultaneously.

METHODS

Site description

This study was conducted at Walker Branch Watershed in the Oak Ridge Environmental Research Park, near Oak Ridge, TN (35°58'N, 84°17'W). The study site is located along the crest of a broad ridge at an elevation of 365 m above sea-level. The site is forested primarily by a mixed-age stand of oak and hickory species typical of the Southern Appalachian region (Hutchison et al., 1986; Johnson, 1989). Mean tree height of the stand is about 21.5 m (Hutchison et al., 1986), and rainfall averages 136 cm annually (National Oceanic and Atmospheric Administration, 1989). The site is equipped with a 44 m scaffold-type walk-up tower extending above the canopy, and an automated tram system instrumented for measuring radiation as described by Baldocchi et al. (1984). The LAI and woody silhouette-area index (WAI) have been estimated at the site both directly (e.g. stratified clip method) and indirectly at the forest floor and at various levels within the canopy in the past (Hutchison et al., 1986), making it an appropriate site for comparison of estimation methods.

In this study, LAI was estimated during the full-leaf period (late summer) of 1989 and periodically throughout the leaf-fall season using three methods: (1) direct calculations from weekly litterfall, in which total leaf areas were estimated using relationships of dry weight to leaf area for each species; (2) indirect estimation using direct beam penetration data collected with a photosynthetically active radiation (PAR) sensor on the automated tram system; (3) indirect estimation from diffuse light penetration data collected with the LAI-2000 Plant Canopy Analyzer.

Comparisons were made between estimates from the Plant Canopy Analyzer and litterfall for six sample dates, and comparisons of these with tram estimates were made for five dates.

Data collection

Direct litterfall measurements

Plastic, 4.7 l baskets with an opening diameter of 0.28 m were used to collect litterfall. Several small holes were drilled in the basket bottoms to ensure drainage, and the baskets were secured to wooden stakes so that, once in place, the opening remained level. Thus, the baskets provided a sample area corresponding to 0.061 m^2. On 20 September, a total of 12 collectors were arranged

approximately 10 m apart in two rows adjacent to the tram system and in three rows radiating from the tower. Negligible leaf fall had occurred at the site before this date. Leaf litter was collected approximately weekly from late September 1989 to mid-January 1990, with the last leaf fall occurring in late December. Samples were labeled by basket number and date, and leaves were oven-dried, sorted by species, and weighed. Previously derived area-to-weight relationships (Table 1) for most species found on the site were used to estimate the total leaf area collected and LAI for each collector and for the site. An average area-to-weight ratio was used for minor species without known conversion factors.

Indirect estimates using direct solar radiation

Assuming foliage elements are randomly distributed within the canopy, the probability that light traveling along some path will make n contacts with foliage is a function of leaf area (L) and can be described by the Poisson probability density function (Nilson, 1971). The probability of noninterception ($n=0$) at solar zenith angel θ ($0°$ is vertical) is

$$P_0(\theta) = \exp[-G(\theta)L/\cos\theta] \tag{1}$$

$G(\theta)$ represents the mean projection of a unit leaf area in the direction of the beam and onto a plane normal to the beam. G is a function of both θ and the leaf inclination distribution, but at $\theta = 57°$, $G \approx 0.5$ for any distribution of leaf

TABLE 1

Weight-specific leaf area for species found on the study site, obtained by regression of dry weight on measured leaf area for subsamples of 1988 and 1989 litterfall: area of each collector $=0.0613$ m^2

Species	Area wt^{-1} (m^2 kg^{-1})	S.E.	Total Collected (kg)	LAI
Beech	25.63	0.945	0.00046	0.016
Black gum	13.85	0.428	0.00649	0.122
Black oak	11.04	0.446	0.00067	0.010
Chestnut oak	12.09	0.282	0.04074	0.670
Dogwood	15.52	0.565	0.00007	0.001
Hickory	12.00	0.411	0.00812	0.132
Red Oak	9.98	0.272	0.02842	0.385
Persimmon	16.64	na	0.00035	0.008
Red maple	16.53	0.542	0.08038	1.806
Sourwood	25.98	1.356	0.00223	0.079
Tulip poplar	13.43	0.313	0.00464	0.085
White oak	10.34	0.214	0.10990	1.544
Other[a]	14.17	1.536	0.00094	0.018
			Total LAI $=4.89$	

[a]Other species include cherry, sassafras, and miscellaneous.

inclinations (see Ross (1981)). Letting transmittance or $T(\theta)$ represent the fraction of beam penetration, eqn. (1) becomes

$$L\,G(\theta) = -\cos\theta \ln T(\theta) = K(\theta) \tag{2}$$

(Nilson, 1971; Lang and Xiang, 1986). $K(\theta)$ has been called contact number (Lang and Xiang, 1986) because it is analogous to the mean number of contacts with foliage that a thin probe (or a light ray) would make traveling through the canopy in a fixed direction. As light travels along paths at increasing zenith angles (i.e. approaching horizontal), transmittance should decrease because the path length through the canopy increases. The effect that this difference in path length has on transmittance can be corrected simply by dividing by the path length. Thus, the contact number $K(\theta)$ is defined as the log of the transmittance (or gap fraction) along a particular path divided by the distance light travels along that path length within the canopy (calculated as cos θ, assuming a vertical path is one unit).

Lang (1986, 1987) demonstrated the utility of approximating the contact number as a linear function of θ. Regressing K on θ yields

$$K = a + b\,\theta \tag{3}$$

where a is the intercept and b is the slope of the linear regression. Miller (1967) showed that L is related to K as

$$L = 2 \int_{0}^{\pi/2} \sin\theta\, K(\theta)\, \mathrm{d}\theta \tag{4}$$

By substituting eqn. (3) into eqn. (4) and integrating, Lang (1987) expressed LAI as

$$L = 2(a + b) \tag{5}$$

As Lang reported, this analysis is equivalent to interpolating a value of K at 1 radian (57°) and applying eqn. (2) with $G = 0.5$.

In our application, beam transmittance was determined as the ratio of beam PAR measured below and above the canopy. The light environment below a forest canopy exhibits appreciable spatial variability (Figs. 1 and 2), so spatial averaging is necessary to obtain representative results. Below-canopy beam PAR was measured at 1 m above the ground on the moving tram system. The tram is supported on parallel cables that extend from one spur tower adjacent to a 44 m walk-up tower, to another triangular support tower 30 m away. The cables were oriented 72° east of north. The tram package traversed through the canopy at a rate between 0.03 and 0.05 m s^{-1} and was equipped with two Li-Cor quantum sensors (model 190S). One sensor measured total incoming radiation. The other was equipped with an occulting band to measure background diffuse radiation. Above-canopy PAR was measured at the tower
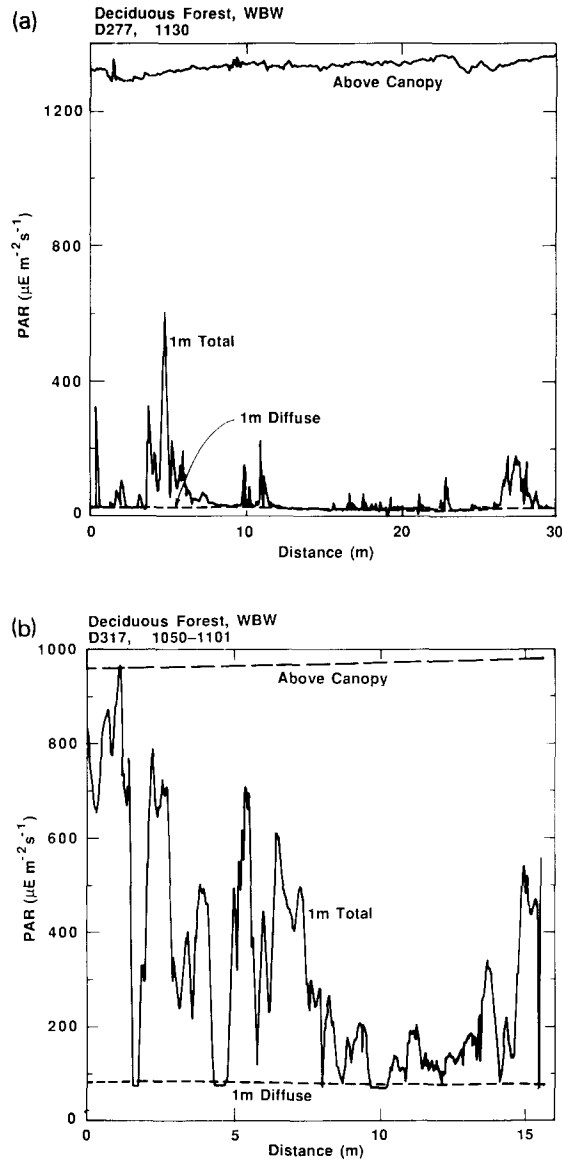
Fig. 1. Total above- and below-canopy beam and diffuse PAR data shown was collected with the tram system on (a) calendar day 277 and (b) calendar day 317. The minimum total PAR approximates diffuse radiation for the intervals shown.

height of 44 m. Measurements were taken and data recorded at 1 s intervals with a Campbell 21-X data logger (Campbell Scientific, Logan, UT).

Solar angles were computed using an algorithm published by Walraven (1978). The plant area index or PAI, which includes projected area of woody elements as well as leaves, was determined using eqn. (5) for five different
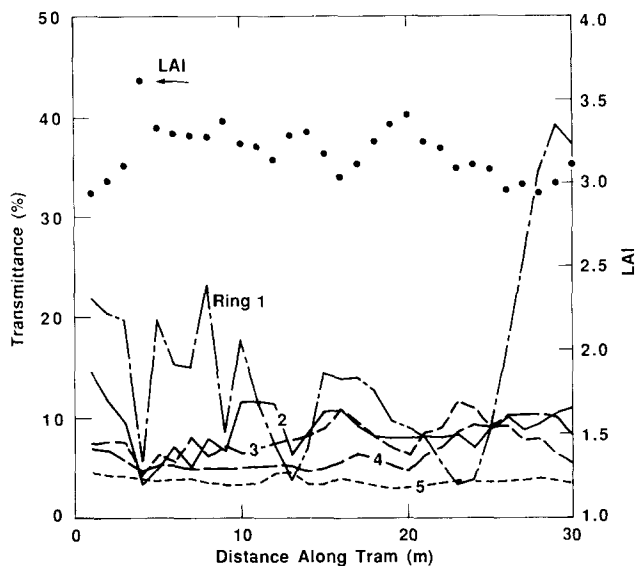
Fig. 2. Per cent transmittance recorded by each ring of the LAI-2000 Plant Canopy Analyzer at 1 m intervals along a 30 m transect beneath the canopy reflects the spatial variability of the canopy. Increasing path lengths decrease both the magnitude and variability of the transmittance. Ring 1 ranges from 5 to 40% whereas ring 5 is nearly constant at 5%. The accompanying estimates of LAI (using eqn. (5)) demonstrate the inverse relationship between leaf area and light transmittance. These data were collected on calendar day 263.

days from 4 October to 15 November 1989, as the canopy changed from near full-leaf to near leafless.

Our intent was to measure beam PAR as the difference between total and diffuse PAR. This was successfully accomplished above the canopy with Li-Cor quantum sensors equipped with and without an occulting band. Unfortunately, it is often necessary to resolve very small differences in signal when the below-canopy sensor package is in the shade (Figs. 1(a) and 1(b)). Consequently, small errors in calibration can cause negative values of beam PAR, which yield undefined logarithm values. To minimize such errors, below-canopy beam PAR was determined using only the instrument that measured total PAR. We assumed that diffuse radiation was equal to the minimum PAR level detected by that instrument on clear days for short time periods (less than 10 min). Our tests showed that this was indeed a reasonable assumption (Figs. 1(a)and 1(b)).

The estimates of beam PAR below the canopy assume that no scattered radiation is detected. Leaves in the upper canopy (65% of foliage) in this forest stand typically absorb between 85 and 100% of incident PAR (Hutchison and Baldocchi, 1989), so the contributions from scattered radiation along the solar path should be negligible. Contamination from diffuse radiation

would necessarily enter along the same solid angle as the beam and thus is confined to a very small fraction of the hemisphere. In addition, measurements were taken only on clear days when the diffuse fraction of PAR measured as a beam is less than 20%. Thus, scattered and diffuse radiation have a relatively small influence on the estimate of beam radiation at the forest floor.

The contact number in eqn. (2) was estimated by averaging the natural logarithm of transmittance values over a 10 min period ($\overline{\ln T}$ with $n \approx 600$). Because LAI is directly proportional to $\ln T$, the accuracy of the LAI estimate depends on using an appropriate method for obtaining a value of $\ln T$. The estimate of transmittance (T) for the entire canopy must average the spatial variability that inevitably occurs in point measurements of T. Several different averaging methods have been reported for obtaining values for $\ln T$ (Baldocchi et al., 1985; Lang et al., 1985; Lang and Xiang, 1986). The two critical issues in determining an expected value for $\ln T$ are: (1) how to deal with the zero transmittance values which result, in part, from limitations in sensor sensitivity; and (2) at what stage to take the logarithm of T.

The issue of zero values of T (i.e. undefined logarithms) can be addressed in two ways. Lang and Xiang's (1986) theoretical approach involves choosing a sampling length over which to average T such that the probability of a zero result is negligible (approximately 10 times the characteristic leaf width). In practice, values of T less than the sensor's lower limit of resolution were set to the limiting value. Assuming a random leaf distribution within this small area, Lang and Xiang then estimated LAI using the average of the logarithms of these localized average T values ($\ln \overline{T}$ rather than $\overline{\ln T}$).

The minimum photon flux density which could be resolved by our sensors was 0.1 μE m^{-2} s^{-1}. In the analysis of the beam transmittance data from the present study, this minimum value was substituted for all zero values of T, and LAI was estimated using $\overline{\ln T}$. We justified the use of this approach based, in part, on the observation that leaves within the site are clumped even on very small scales. We found that the various methods for estimating $\ln T$ produce LAI estimates that do not differ greatly. When we analyzed a subset of our data using the method of Lang and Yueqin (1986) and our method described above, a regression of the LAI estimates yielded a coefficient of determination near one, with our method yielding estimates of 0.25 units higher (and closer to the litterfall estimates) than those estimated with linear subaveraging.

Indirect estimates using the LAI-2000 Plant Canopy Analyzer

The LAI-2000 Plant Canopy Analyzer is a portable light sensor system designed to measure diffuse light from several zenith angles simultaneously. Each sensor consists of five concentric, light-detecting rings that receive radiation from different sky sectors centered around the angles 7, 23, 38, 53 and 68°

(Fig. 3). Because measurements are made of diffuse rather than direct light, all five zenith angles can be sampled simultaneously. The ratio of light levels measured above and below the canopy gives the transmittance for each sky sector. Figure 2 shows data collected at 1 m intervals, for each of the five rings, along a transect and illustrates the relationship between transmittance and estimated LAI.

Assuming a Poisson model of light penetration (i.e. that foliage elements are distributed randomly in space), measured transmittances for each zenith are used to calculate a mean contact number $K(\theta)$, according to eqn. (2), for that canopy sector. PAI is then computed by integrating eqn. (4) using the approximation (Li-Cor, 1989)

$$L = 2[0.03K(7°) + 0.10K(23°) + 0.16K(38°) \qquad (6)$$
$$+ 0.21K(53°) + 0.50K(68°)]$$

This solution is approximately equivalent to weighting the mean contact numbers of each canopy sector by the proportional area of that sector (i.e. the area of the annulus viewed in that sector divided by the total area viewed in all sectors).

This method avoids explicit use of the G function, which requires a priori knowledge of the distribution of leaf inclinations. In addition, LAI-2000 software allows computation of PAI using any pair or subset of zenith angles and includes the option to calculate PAI using eqn. (5). Results from eqns. (5) and (6) are approximately equivalent when data from all five rings are included but may differ for various subsets of rings.

As with the direct beam measurements, a necessary assumption is that any transmitted or reflected radiation included in the below-canopy readings is negligible. To this end, the sensors are filtered to accept only wavelengths below 490 nm because vegetation transmits very little light in this region (Li-Cor, 1989). On days when the sun is unobstructed, direct beam radiation must be blocked from the sensor using a view restrictor. A second assumption
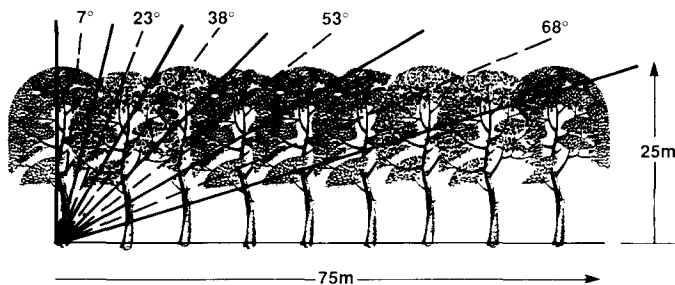

Fig. 3. The five regions of diffuse light interception for the LAI-2000 Plant Canopy Analyzer's light-detecting rings (1–5) are centered on zeniths 7, 23, 38, 53 and 68°. (Note that the path length for the sky sector centered on 68° is approximately three times the canopy height.)

is that sky brightness is azimuthally uniform, as is the case under a uniformly overcast sky. Nonuniform brightness results in portions of the canopy being weighted too heavily (Li-Cor, 1989). Errors associated with sky conditions are detectable and may significantly affect PAI estimates (see below).

Another important consideration when using gap fraction methods, the LAI-2000 in particular, is topography. Because the range of view for the LAI-2000 is approximately three times the canopy height ($1/\cos\theta$ times canopy height; see Fig. 3), changes in topography within this area will affect the expected transmittance. Distant hills which obscure portions of the sky would have a similar effect. Because this study site is located along a ridge with only slight slope, topography will not be considered a significant source of error for either indirect method.

Two instruments are normally used to calculate the light transmittance through a forest canopy. A remote instrument (A) positioned above the canopy or in an unobstructed clearing can be programmed to log data automatically while a second sensor (B) is operated manually below the canopy. Temporally paired readings from the A and B units are then used to calculate the diffuse transmittance.

In this study, the LAI-2000 was used to estimate LAI above each of the 12 litterfall collectors described earlier. LAI measurements were also made at 1 m intervals along the 30 m tram-line and along a vertical transect extending above the canopy using the 44 m walk-up tower. Readings were taken approximately weekly between 20 September 1989 and 15 January 1990. For tower measurements, the A sensor was placed above the canopy and was extended as far outside the structure as possible. A 90 or 180° view restrictor was in place to block the tower from the sensor readings. The sensors were then calibrated to each other before sampling. At each level of the tower (2 m intervals), three observations were made with the B unit held outside the tower and oriented in the same direction as the A unit.

Readings over the litter collectors were generally taken with the A unit positioned on the tower as described, although above-canopy readings were occasionally taken in a nearby raingauge field instead. Two observations were taken with the B sensor directly above each litterfall basket. Data were transferred to a personal computer each day, and the A and B files were combined and analyzed. LAI was derived from the initial PAI by subtracting the estimate of silhouette-area index for the woody biomass (0.60) obtained at this site by Hutchison et al. (1986).

RESULTS

Absolute leaf area

Estimates of LAI obtained using each method are presented in Table 2.

TABLE 2

Comparison of mean leaf area index estimates from litterfall with estimates obtained from direct beam, and diffuse light data (LAI-2000, 0–75°) using the Poisson model

Calendar day	Sky[a]	Litterfall		Direct Beam				Diffuse Light	
		LAI	s_L[b]	LAI	s_K	s_L	r^2	LAI	s_L
263	S	4.89	0.95					2.91	0.28
270	S							2.49	0.28
277	S			3.79	0.070	0.80	0.65	2.46	0.28
279		4.76	1.01						
285	S	4.56	0.96					2.24	0.28
291	C	4.21	0.83					2.24	0.21
294				3.19	0.099	0.91	0.69		
297				3.45	0.035	0.50	0.80		
299	S	3.88	0.92					1.70	0.14
306	C	1.89	0.53					0.71	0.07
312		0.69	0.31						
313				1.44	0.049	0.62	0.34		
317				1.32	0.061	0.27	0.83		
320		0.14	0.31						
333		0.00	na						
365	MC	0.00	na					0.13	0.07
015	C	0.00	na					0.13	0.07

[a]Sky conditions: S = sunny; C = uniformly cloudy; MC = mostly cloudy.
[b]s = standard deviations for LAI (L) or contact number (K).

Litterfall collections yielded the highest and presumably most accurate LAI estimates throughout the season, with a site average (at full leaf) of 4.89 (±0.95). An earlier, direct-measurement study in 1978 at this site (Hutchison et al., 1986) found LAI to be 4.9.

By Lang's regression method (eqn. (5)), using direct beam transmittance data, full PAI was estimated to be 4.39 ± 0.80. Assuming WAI is 0.60, this yields an LAI value of 3.79 ± 0.80, which is not statistically different from the litterfall estimate. However, the means do exhibit an obvious bias. Because LAI is estimated from the contact number (K) interpolated at 1 radian, standard deviations for LAI (s_L for direct beam data in Table 2) are computed, based on eqn. (5), as $\sqrt{(c^2+e^2)}$ or $\sqrt{(2^2+\sigma_K{}^2)}$.

In comparison with litterfall, the diffuse transmittance method underestimated leaf area at this site by about 45% when transmittances from all five sky sectors were considered (Table 2 and Fig. 4). This estimate, 2.91 ± 0.28, is significantly lower than the litterfall estimate ($\alpha = 0.05$) but not statistically different from the direct beam estimate. The result improves as the lower zenith rings are omitted (Fig. 5), with readings between 0 and 30° (rings 1 and 2 alone) yielding a full-leaf mean of 4.17 ± 0.73, which is not statistically different from 4.89 ± 0.95.
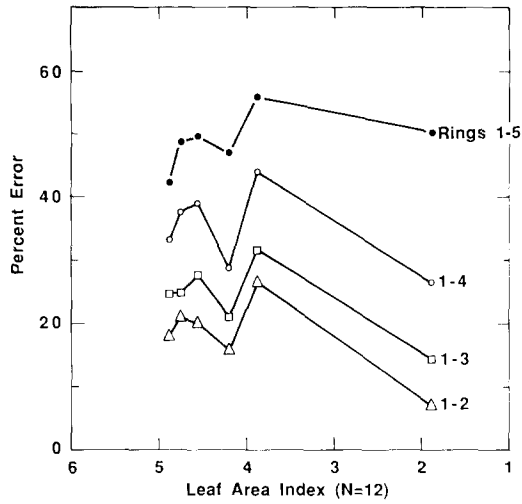
Fig. 4. The accuracy of LAI estimates obtained with the Plant Canopy Analyzer decreases with the inclusion of rings at higher zeniths (approaching horizontal). The best estimates were obtained from rings 1 and 2 for all stages of leaf fall.
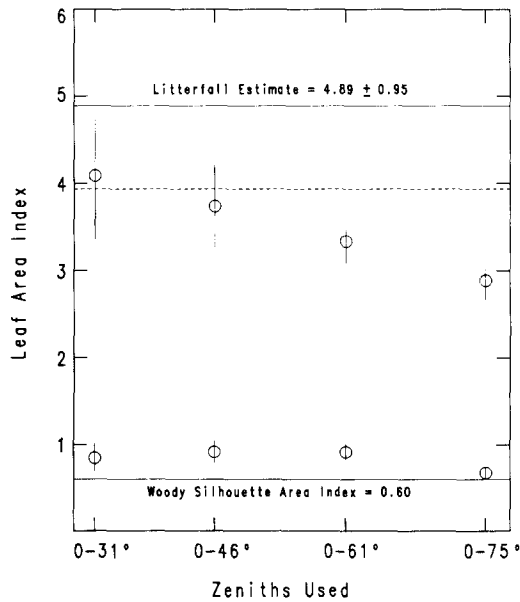

Fig. 5. Accuracy of indirect LAI and WAI estimates, computed from diffuse transmittance, relative to direct estimates. Means ($n = 12$) for the four subsets of zeniths represent full-leaf LAI calculated using the Plant Canopy Analyzer on 20 September 1989. WAI estimates were obtained on 29 December 1989. The LAI of 4.89 ± 0.95 is a mean based on litterfall from the same locations. The WAI value of 0.60 was established by Hutchison et al. (1986).

In practice, we found it helpful to discard values from ring 5 (61–76° from zenith) of the LAI-2000. Transmittance values along this beam angle were consistently higher than expected. This could be attributed to scale-dependent attributes of the forest canopy for which no account has been taken, such as an increasingly uniform distribution of foliage elements (tree canopies) over long distances. Other possible explanations are significant topographic effects and potential errors in the above-canopy data.

Spatial and temporal variability in LAI

The temporal variability of LAI was described equally well by both indirect methods. Figure 6 shows the relative decrease in LAI through the season for each method. This pattern reflects the phenology of the dominant species and is consistent with other studies from the watershed (Grizzard et al., 1976). For the diffuse penetration data, the pattern of increasing underestimation with the inclusion of lower zenith rings (i.e. rings 4 and 5) holds for all values of LAI (Fig. 4).

Spatial variability in light transmittance beneath the canopy is shown in Figs. 1 and 2. Litterfall estimates and estimates made with the LAI-2000 above each litterfall collector (Fig. 7) indicate a comparable degree of LAI variability within this site. Coefficients of variation for the litterfall data from all 12 collectors range from 19 to 28% , and for the LAI-2000 from .13 to 18% (27 September–2 November). Coefficients of variation from the direct beam PAR method are between 10 and 30% and are consistent with the other methods. All three methods indicate that the spatial variability in leaf area at this scale remained approximately constant as the total leaf area decreased (i.e. there
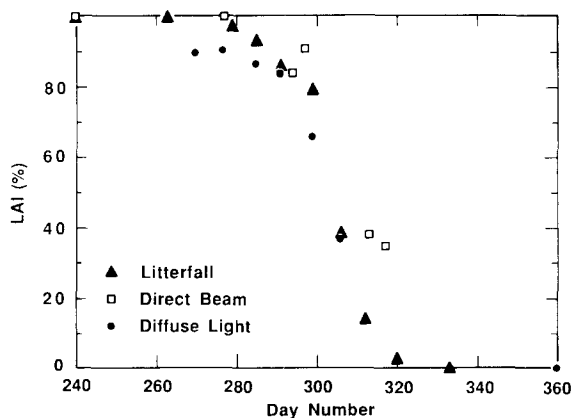

Fig. 6. Per cent LAI remaining on each sample date as estimated by direct beam penetration (diamond), and diffuse radiation penetration (circle) compare well with estimates from litterfall (triangle).
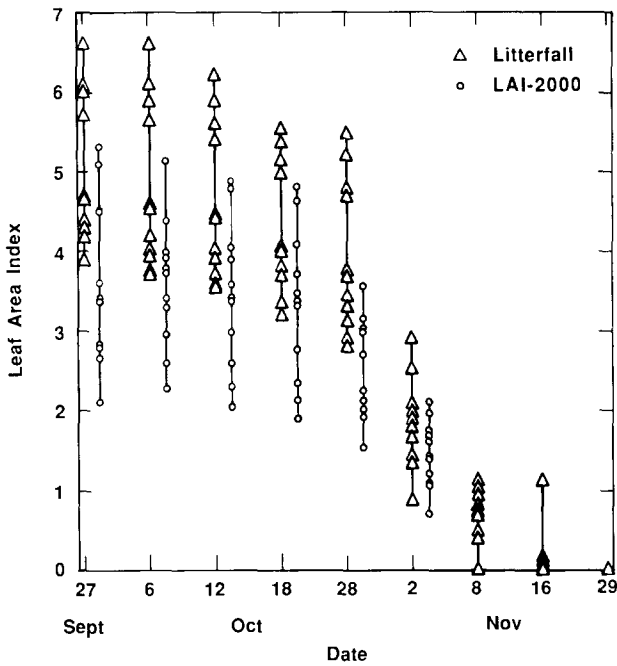
Fig. 7. Comparison of LAI estimates from litterfall (triangle) and diffuse radiation measurements using the LAI-2000 (circle) for 12 locations and six sample dates indicates similar degrees of variability within the site. Indirect estimates are based on rings 1 and 2 only.

was no significant temporal pattern in the degree of canopy heterogeneity), at least until LAI fell below one.

Figure 8 compares the vertical distribution of LAI measured by the LAI-2000 (2 m intervals) with direct measurements made in 1980 (0.5 m intervals) by Hutchison et al. (1986). The indirect estimates differ most in the upper canopy, above 15 m. The observation of greater clumping in the crowns (Baldocchi et al., 1985) is consistent with our interpretation of one cause of the underestimation as discussed below. This indirect method can be easily used to obtain information on LAI profiles, provided an appropriate model of leaf inclination and clumping is applied.

Woody area index

Estimates made during the leafless period correspond to the woody silhouette-area index. As with LAI, inclusion of all five rings in the analysis (Poisson model) gave a significantly lower estimate than the other subsets ($\alpha = 0.05$), but the estimates from rings 1–3 and 1–4 were higher than that from rings 1 and 2 alone. Although the variation was small, all estimates were
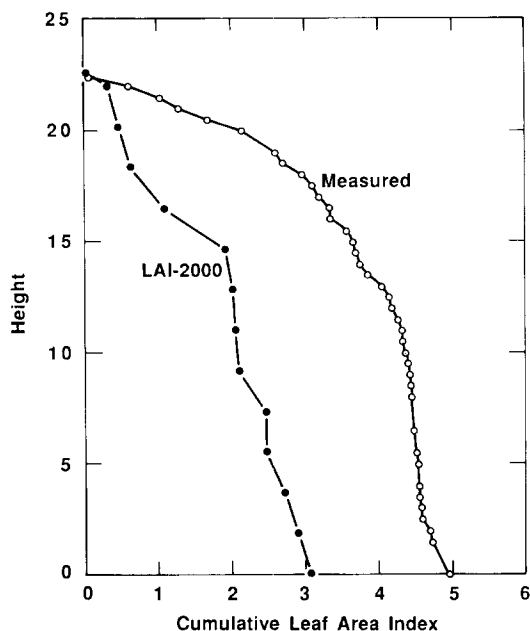
Fig. 8. A vertical profile of LAI was obtained with the LAI-2000 at 2 m intervals and compared with means at 0.5 m intervals obtained by direct sampling in 1980 and 1981 (Hutchison et al., 1986). With the indirect method, clumping of foliage causes the Poisson model to underestimate leaf area, with increased clumping in the upper canopy resulting in poorest agreement above about 14 m.

slightly higher than the 0.60 established by Hutchison et al. (1986) in 1980 and 1981 (Fig. 5).

DISCUSSION

The basic concepts behind both the direct beam and diffuse light methods are well proven. The use of light to probe the canopy from different angles provides useful information on the structure of the canopy, given an adequate model to interpret the data. However, both the direct beam and diffuse light transmittance methods underestimated leaf area in this oak–hickory forest when analyzed using the methods of Lang (1986, 1987) and Li-Cor (1989). Although both methods captured the spatial and temporal variation in canopy LAI in a qualitative sense, both failed to produce a satisfactory quantitative estimate of total LAI. The LAI-2000 Plant Canopy Analyzer has produced accurate, quantitative estimates of LAI in agricultural crops (Li-Cor, 1989) although the results at our deciduous forest site are less than satisfactory.

One source of error for the diffuse light method is the sky condition. For instance, the 8% decrease in LAI between day 285 (sunny) and 291 (cloudy)

was not reflected by the Plant Canopy Analyzer (Table 2). Comparison of estimates for day 299 made at midday and dusk shows an almost 20% increase in the latter estimate. This is presumably due to diminished direct beam interference. However, data collected at a nearby site on days 305 (sunny) and 306 (cloudy) produce identical estimates. The 23% difference between the direct beam estimate (3.79) and the diffuse light estimate (2.91) is another possible indicator of the error related to sky conditions. Although no generalizations can be drawn from our results, sky conditions are clearly important for the diffuse light method, with the potential error (between 8 and 20%) dependent on an interaction between those conditions and site-specific canopy characteristics.

Considering the entire season, the LAI-2000 estimates were linearly related to the direct litterfall estimates (Fig. 9). Linear regression (using all rings) yields $L_{litter} = 1.86 \times L_{LAI\text{-}2000}$ with $r^2 = 0.97$. Because of this linear relationship between the indirect, LAI-2000 estimates and the litterfall estimates, one solution to the underestimation problem is simply to apply the correction factor of 1.86. A similar scaling factor for direct beam estimates would be 1.16. Although this approach does not help explain the causes of the underestimation, it is straightforward and should give reliable LAI estimates for similar forests.

The direct beam approach implemented here is limited by some crude design features. Improvements can be made by filtering out errors introduced by the reception of scattered light. This can be done by installing an optical filter that eliminates light above some threshold wavelength (Lang chose 430 nm as this threshold). There is also some concern about the system's ability
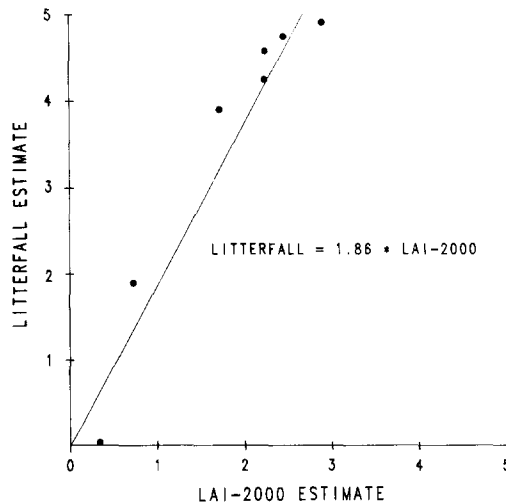
Fig. 9. Linear regression of indirect LAI estimates from the LAI-2000 on direct estimates from litterfall provides a linear scaling factor of 1.86.

to measure beam transmittances precisely through optically thick canopies (as when LAI is great or the sun angle is low). It is especially difficult to determine the beam flux density well under low light conditions when it is evaluated as the difference between total and diffuse radiation.

A critical assumption in the use of the Poisson distribution for calculating LAI from light transmittance is that the plant foliage is randomly distributed, at least on a small scale. The poor performance of both methods in predicting LAI using a Poisson model suggests that this assumption may be inappropriate for forest canopy structure at this site. At large scales, it is obvious that foliage is clumped into individual tree canopies and that gaps exist. Such discontinuities have been addressed by Lang and Xiang (1986) for cases where leaves are randomly distributed locally. Baldocchi et al. (1985) and Kruijt (1989) showed that the foliage may be densely clumped at very small scales within an individual canopy. At this site, localized clumping is greatest in the upper canopy, where typically more than 85% of radiation interception occurs (Baldocchi et al., 1985). Relative to a random leaf distribution, clumping enhances the probability of light penetration, leading to an underestimate of LAI if randomness is assumed. Both small- and large-scale clumping undoubtedly contribute to the error we observed.

Given that foliage is clumped even at a very small scale, a more sophisticated approach would be to consider the leaf cluster rather than the single leaf as the model canopy element. Such leaf clusters appear to have fairly constant dimensions (Kruijt, 1989) and would be relatively simple to quantify. If the leaf clusters are randomly distributed and their characteristics known (e.g. leaf area per cluster), the Poisson model could be applied and the results scaled to represent total leaf area. This approach has been used successfully in conifer stands (Li-Cor, 1990).

Alternatively, the negative binomial model estimates the probability of light penetration in canopies that have clumped foliage and can be inverted to estimate LAI:

$$L = -\frac{\ln T(\theta) \cdot g}{\ln[1 + g\, G(\theta)/\cos \theta]} \tag{7}$$

where g is the clumping factor, θ is the bean angle from zenith, and $T(\theta)$ and $G(\theta)$ are defined as before (Acock et al., 1970; Nilson, 1971). The critical difference between the Poisson model (eqn. (4)) and the negative binomial model is in the treatment of a 'leaf layer'. The Poisson model assumes that a canopy having a given LAI (L) consists of a large number (N) of statistically independent horizontal layers, each with thickness $dL = L/N$, and the probability of more than one contact of the light beam with a leaf element within a single thin layer (dL) is very low. The negative binomial model assumes that a canopy having a given leaf area (L) consists of a finite number (N) of equal

and statistically independent layers in which $N=L/dL$ and more than one contact within a layer is possible. In the negative binomial model, dL can be considered a clumping factor (equivalent to g in eqn. (7)), with higher values of dL indicating greater foliage clumping. As the clumping factor approaches zero, the negative binomial distribution converges to the Poisson distribution (Nilson, 1971).

In previous work using the binomial model, the clumping factor for the canopy at our study site was estimated to be 2.42 (Baldocchi et al., 1985). This large value of g resulted from taking the log of $\overline{T(\theta)}$ averaged across 30 m rather than averaging ln $T(\theta)$. If we re-evaluate g using the direct beam transmittance data and $G(\theta)$ values determined from site-specific leaf inclination data (Baldocchi et al., 1985), we find that $g=1.6$ yields an LAI that matches the litterfall estimate (4.89). Because the re-evaluated g is still clearly non-zero, we must conclude that clumping of foliage has contributed to the underestimation of LAI based on the Poisson distribution.

Applying the negative binomial model with $g=1.6$ to out diffuse light transmittance data also produces good correspondence with litterfall (Table 3 and Fig. 10). Calculations using all sky sectors produces an average LAI of 4.34 ± 0.36 (PAI$=4.94$), which is within 12% of the litterfall estimate of 4.89. This value compares with 2.91 using the Poisson model. Thus, the negative binomial model, by accounting for foliage clumping, provides a more accurate LAI estimate than does the Poisson model (Fig. 10).

In a similar study, Neumann et al. (1989) found that applying the Poisson model to hemispheric photographs underestimated LAI in a maple–aspen forest by about 50%. Using the negative binomial model with the clumping factor of 2.42 from Baldocchi et al. (1985), they obtained relatively good

TABLE 3

LAI estimates based on the negative binomial model using diffuse light penetration measurements (from the LAI-2000) in comparison with direct estimates from litterfall

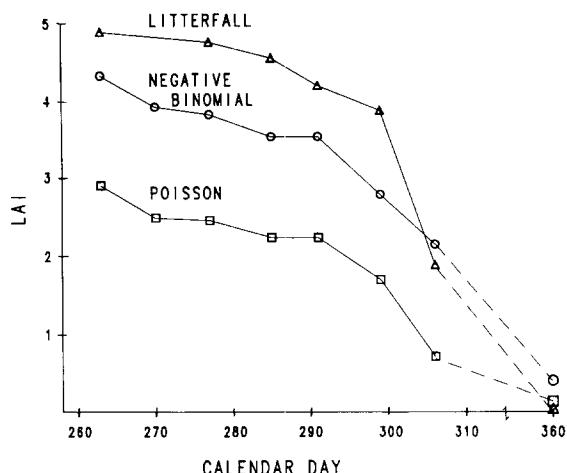| Day	Negative binomial ($g=1.6$)		Litterfall	
	Mean	s_L[a]	Mean	s_L
263	4.34	0.35	4.89	0.90
270	3.93	0.35		
277	3.83	0.32	4.76	0.99
285	3.54	0.22	4.56	0.96
291	3.54	0.32	4.21	0.83
299	2.79	0.32	3.88	0.90
306	2.15	0.66	1.89	0.52
363	0.38	0.26	0.00	na

[a]$s=$standard deviation for LAI (L).

Fig. 10. Comparison of LAI estimates from litterfall with Poisson and negative binomial model estimates from LAI-2000 data using zenith angles 0–75°. Comparison of the estimate from day 285 (sunny) with day 291 (uniformly overcast) suggests the underestimation associated with sunny sky conditions.

agreement with litterfall while LAI was high, but they reported an increasing overestimate as leaf fall progressed. This result is consistent with our findings.

Both the Poisson and negative binomial models slightly overestimated LAI (corresponding to WAI) in the leafless forest. Because the positive binomial model (eqn. (8)) corresponds to uniformly distributed foliage (Nilson, 1971; Ross, 1981) it may better represent the distribution of individual trees and, thus, the distribution of woody area in a leafless forest:

$$L = \frac{\ln T(\theta) \cdot g}{\ln[1 - g\, G(\theta)/\cos\theta]} \tag{8}$$

Using the mean ln T for ring 4 (53°) and $G=0.5$, an estimate of $g=0.578$ (a uniformity parameter in this case) was established for the leafless forest. Because g is again nonzero, we conclude that the more uniform spacing of woody plant parts should be accounted for if indirect methods are applied to estimate WAI.

CONCLUSIONS

Indirect methods of estimating leaf area based on the inversion of radiation penetration models are extremely useful for rapid, non-destructive determination of LAI and other canopy properties. However, realistic characterization of canopy architecture by the analytical model is critical, and violation of the assumptions of a specific model can lead to significant errors in the

absolute accuracy of the estimates. Light penetration models based on an assumed random distribution of canopy elements can be inaccurate, generally underestimating LAI when leaf spatial distributions are clumped. Thus, techniques based on the inversion of light penetration models must be used judiciously in a canopy where the clumping of leaves and branches can cause foliage elements to depart from a random (Poisson) distribution.

Analysis of both direct beam and diffuse light data using techniques based on the assumption of a random foliage distribution underestimated absolute LAI in this oak–hickory forest. On the other hand, both techniques provided reliable relative estimates and accurately described temporal changes in LAI. The LAI-2000 also described spatial variability of LAI well.

If characteristics of an appropriate canopy element (e.g. leaf clusters) are known, or an empirical correction factor is available, simple scaling may provide accurate LAI estimates. If leaves are distributed randomly at a small scale, the technique of Lang and Xiang (1986) should account for larger-scale canopy discontinuities. However, when canopy elements are clumped even at a very small scale, the negative binomial model gives a relatively accurate estimate of foliage area by incorporating an empirically derived clumping parameter. For leafless forests, in which foliage elements may actually be uniformly distributed, the positive binomial model may prove more accurate for estimating WAI.

Although refinements in the model and data analysis, or at least linear scaling, are necessary to implement properly the LAI-2000 Plant Canopy Analyzer in forests where canopy elements are not random, it can potentially produce LAI estimates that are both accurate and precise (see Gardner et al., 1981). One advantage over the tram system is that it obtains in a single reading data that require a half-day to collect using the direct beam. Furthermore, its ease of use and portability provide another advantage over many techniques in that both intensive sampling within one site and comparison of distant sites are simple and practical. On the other hand, direct beam techniques are less sensitive to sky conditions and are potentially more adaptable to complex terrain.

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