Laser point-quadrat sampling for estimating foliage-height profiles in broad-leaved forests

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Abstract: A technique for estimating the vertical distribution of foliage area in broad-leaved forests was developed. The technique is similar to optical point-quadrat sampling, where estimates are based on heights to the lowest leaves above numerous sample locations beneath a canopy. In optical point-quadrat sampling, heights to lowest leaves are measured with a telephoto lens. Here, heights were measured using a commercially available laser range-finding instrument. The laser point-quadrat technique was tested in field studies conducted under broad-leaved forest canopies in western North Carolina and east-central Minnesota, U.S.A. Foliage-height profiles obtained by laser point-quadrat sampling were consistent with two of four published foliage-height profiles observed in 1995 at the North Carolina field locations. Total leaf area estimates obtained by laser point quadrats were not significantly correlated with values of leaf area index estimated by recent fall analyses at the North Carolina and Minnesota field locations. Although further evaluation and refinement of the technique is needed, laser point-quadrat sampling shows promise as a means of obtaining foliage-height profiles at a significantly reduced effort and with greater accuracy than methods commonly in use today.

Résumé : Les auteurs ont mis au point une technique pour estimer la distribution verticale de la surface foliaire dans les forêts feuillues. La technique est semblable à l’échantillonnage optique par points-quadrats où les estimés sont basés sur la hauteur des feuilles les plus basses au-dessus de nombreux points d’échantillonnage sous le couvert forestier. Dans le cas de l’échantillonnage optique par points-quadrats, la hauteur des feuilles les plus basses est mesurée avec un téléobjectif. Ici, les hauteurs ont été mesurées à l’aide d’un instrument laser de mesure des distances disponible sur le marché. La technique d’échantillonnage au laser par points-quadrats a été testée dans le cadre d’études sur le terrain réalisées sous le couvert de forêts feuillues situées dans l’ouest de la Caroline du Nord et le centre-est du Minnesota, aux États-Unis. Les profils de hauteur du feuillage obtenus avec l’échantillonnage au laser par points-quadrats sont conséquents avec deux des quatre profils de hauteur du feuillage publiés qui ont été observés sur le terrain en 1995 dans les sites de la Caroline du Nord. Les estimés de la surface foliaire totale obtenus avec l’échantillonnage au laser par points-quadrats n’étaient pas significativement corrélés avec les valeurs de l’indice de surface foliaire déterminé par les analyses récentes de chute de litière dans les sites de la Caroline du Nord et du Minnesota. Quoique la technique doive être évaluée et raffinée davantage, l’échantillonnage au laser par points-quadrats est un moyen prometteur pour obtenir des profils de hauteur du feuillage avec un effort significativement moindre et une meilleure précision que les méthodes généralement utilisées aujourd’hui.

[Traduit par la Réduction]

Introduction

Determining the structure of a forest canopy is an important step in understanding the details of its functional role in the forest ecosystem. Knowledge about the vertical distribution of leaf area is especially critical because of the important role that foliage plays in the cycling of carbon, water, energy, and nutrients through the ecosystem (Ford and Newbould 1971; Hutchison et al. 1986; Ellsworth and Reich 1993; Yang et al. 1999). Relatively few techniques exist for quantifying vertical distributions of leaf area. The techniques that do exist are subject to various limitations (Welles 1990). Advancement of the tools available for assessing canopy structure would be a positive development in fields that study relationships between the structure and functioning of forest canopies.

Here, a technique for estimating the vertical distribution of foliage area is developed that makes use of height measurements obtained with a commercially available laser range-finding instrument. First, techniques for estimating vertical profiles of leaf area are briefly reviewed. Emphasis is placed on an optical point-quadrat method that uses measured heights to the lowest leaves above numerous ground locations beneath a canopy. The method is adapted to make use of height measurements obtained with the laser range finder. An experiment is conducted to test the potential for the use of a laser range finder in assessing vertical profiles of leaf area. Results of the experiment are presented, along with suggestions for future research and development related to this methodology.

Canopy profiles via direct and indirect sampling

Direct sampling is undoubtedly the most laborious
Another direct sampling method involves the observation of vertical distributions of foliage in individual trees, then scaling those observations to the canopy level. Such tree-based sampling schemes involve the measurement of branch heights and branch subsampling to estimate foliage area on a branch by branch basis. This approach was taken by Raulier and Ung (1997) and Magnussen and Boudewyn (1998), although determination of the vertical distribution of leaf area was not the primary goal of either study.

Indirect sampling methods provide the means for obtaining leaf area profiles at a reduced amount of effort compared to direct sampling of foliage. These methods are nondestructive so they can be employed without disturbing other experimental efforts taking place at the same location. One indirect method, the point-intercept technique, is based on the number of times a thin rod or plumb line passed through the canopy touches any leaves (Warren Wilson and Reeve 1959; Ford and Newbould 1971; Vose et al. 1995). The amount of effort required in obtaining such samples, although less than that required for direct sampling, is considerable. In tall canopies work is conducted from scaffold or tower structures so that measurements of the number and location of intercepts along the rod or plumb line can be recorded.

Another indirect method involves the estimation of the cumulative leaf area index (LAI, projected leaf area per unit of ground area) at numerous vertical positions in the canopy. LAI is estimated using an instrument such as the LI-COR LAI-2000 (LI-COR Inc., Lincoln, Nebr.) or from hemispherical or fish-eye photography (Gower and Norman 1991; Chason et al. 1991; Wang et al. 1992; Strachan and McCaughey 1996; Yang et al. 1999). These techniques assume that foliage is randomly distributed throughout the canopy, and underestimate leaf area when foliage is clustered, a practical certainty in deciduous forests of eastern North America. An additional limitation is that they only work well when diffuse radiation dominates, significantly reducing potential sampling opportunities. They can be used to obtain relative vertical LAI profiles assuming that any underestimation is constant at all heights in the canopy. Advantages of these techniques over point-intercept sampling are (i) that they are conducted from the ground and (ii) electronic equipment for estimating LAI allows for automatic data storage. These characteristics simplify the sampling effort and remove a source of potential errors. Still, the apparatus needed to raise the measuring instrument into the canopy is typically cumbersome, which may limit the application to comparatively accessible areas.

Optical point-quadrat sampling is a modification of the point-intercept method. Optical point-quadrat sampling is based on measured heights to the lowest leaves above a set of sample points established on the ground beneath the canopy (MacArthur and Horn 1969). In applications related to forests, a telephoto lens is typically used to measure heights to the lowest leaves (Aber 1979a; Hedman and Binkley 1988; Ellsworth and Reich 1993). As such, the entire sample can be conducted from positions on the ground. The technique assumes that foliage is randomly distributed throughout the canopy, and also underestimates leaf area when foliage is clustered. Regardless, under the assumption that the underestimation is constant at all canopy levels, relative vertical leaf area profiles can be determined that describe the percentage of the total leaf area in each canopy layer (Aber 1979b). The measurement apparatus, a telephoto-lens camera mounted on a tripod, is sufficiently portable to allow application of optical point-quadrat sampling under most field conditions.

Use of a laser range finder

In recent years, hand-held laser range finders have been used increasingly to make measurements related to the practice of forestry. Typical applications in forestry involve navigation, mapping, and dendrometry (Liu 1995; Peet et al. 1997; Williams et al. 1999). A number of researchers have used airborne lasers to measure forest canopies, including Lefsky et al. (1999), who used an airborne laser to estimate foliage-height profiles based on a modification of the optical point-quadrat method. Ground-based laser devices have been used to estimate leaf areas of field crops (Denison and Russotti 1997). Tanaka et al. (1998) used a visible laser in conjunction with a digital charge-coupled device (CCD) camera to map the vertical distribution of biomass in a forest canopy. Welles and Cohen (1996) described a scanning laser designed to measure canopy gap fractions from beneath the canopy called the Leaf Laser (Decagon Devices, Inc., Pullman, Wash.); however, the Leaf Laser was never made commercially available (M. Galloway, Decagon Devices, personal communication).

Given prior work, it may be possible to use commercially available hand-held laser range finders to estimate total LAI or vertical foliage profiles in forest canopies. The use of telephoto lenses has been well established for the latter purpose, but the laser provides an obvious alternative with several potential advantages. First, laser distance measurements are quite accurate. For example, the Criterion 400 laser range finder (Laser Technology, Inc., Englewood, Colo.) measures distances to within 2 cm (standard deviation) for a white target at 50 m. Second, distance measurements can be taken very quickly. With the Criterion 400 mounted on a monopod, the unit can be positioned on the ground and steadied for a measurement to be taken within a few seconds. Third, measurements can be automatically recorded and electronically stored for retrieval to a desktop computer for subsequent analysis. To investigate the potential for hand-held laser-based optical point-quadrat sampling, the following experiment was carried out.

Methods

The Criterion 400 was chosen as the instrument for measuring heights to lowest intercept in the laser point-quadrat survey. This instrument has been used extensively in forestry applications for nearly a decade. A Criterion 400 unit was available for our use for the duration of this experiment. Near the end of the experiment, we
gained access to another laser instrument, the Impulse (Laser Technology, Inc., Englewood, Colo.), with similar specifications and used it on a limited basis for comparison. Relevant specifications of the instruments are as follows: range, 3–500 m for the Criterion 400 and 0–500 m for the Impulse; beam divergence, 3 milliradians or 9 cm wide at range 30 m; range resolution, 0.01 m; and range standard deviation, 0.02 m to a white target at 50 m range. Because laser point quadrats are unable to distinguish between plant tissue types, measurements made pertain to plant area index (PAI), which is assumed to be equivalent to LAI in this study.

Study sites

Two locations were chosen for data collection, both corresponding to research sites where recent (within 6 years) observations of total leaf area index were available. Field locations were chosen that matched the studies of Vose et al. (1995) and Bolstad et al. (2001). The first site was the Coveeata Hydrologic Laboratory in the southern Appalachians of western North Carolina. The Coveeata study locations were chosen to facilitate comparison of results obtained from the laser point-quadrat method to the foliage profiles Vose et al. (1995) obtained by counting plumb line intercepts. The second site was the Cedar Creek Natural History Area in east-central Minnesota. Field locations at Cedar Creek were chosen to coincide with field plots on which total LAI measurements had been made from litter collection data in previous years (unpublished data). The Cedar Creek plots were selected to include canopies across a range of litter fall based LAIs, so that the relationship between litter fall and laser point-quadrat LAI estimates could be examined.

Both sites are comprised largely of deciduous species, mainly oaks (Quercus spp.), with several maple species, especially red maple (Acer rubrum L.) present to some extent. Major canopy species at Coveeata are listed by Vose et al. (1995). Most plots at Cedar Creek were established under canopies composed of oaks and northern hardwood species (Acer rubrum, Ostrya virginiana (Mill.) K. Koch, Prunus serotina Ehrh., Quercus ellipsoidalis E.J. Hill, Quercus macrocarpa Michx., and Quercus rubra L.), although largtooth aspen (Populus grandidentata Michx.) was a major overstory component of one field plot examined there.

Sampling method

Measurements at Coveeata were made between June 17 and June 19, 1999. Measurements at Cedar Creek were made between August 19 and August 18, 1999. Timing of measurements was intended to coincide with the part of the growing season during which maximum leaf area was displayed in the canopy. As such, spring leaf expansion was complete prior to the first sampling dates, and the latest observations were conducted prior to the onset of autumn leaf senescence. Plot centers were established at nine previously measured field locations at Coveeata and nine at Cedar Creek.

The intended plot size was roughly 100 m² in a 10 x 10 m configuration. We increased the plot sizes to 169 m² (13 x 13 m) after several trials to insure that an adequate number of point quadrats would be taken at each field plot. Field workers traversed the area of the plot in a regular grid pattern, stopping every 10–13 cm to take a measurement. The grid size was chosen to correspond roughly with the length of a small footstep, so that the Criterion 400, mounted on a monopod 1 m tall, could be placed alongside the observer on each successive footstep. Based on this grid size, roughly 1000 laser point quadrats were to be measured on each plot. The monopod was set on the ground at the point of measurement, and leveled to aim the laser vertically. All measurements were automatically logged into a field computer.

The Criterion 400 makes an audible warning and records an error code if either (i) the beam is intercepted within 3 m from the instrument or (ii) the beam does not intercept any solid object within 500 m (i.e., an open sky “hit”). Upon hearing the error warning, field workers made an ocular determination of whether the beam was intercepted by low vegetation or penetrated through the canopy to open sky. Open sky hits were tallied manually. One plot at Cedar Creek was measured using an Impulse laser range finder. The Impulse is not subject to the same 3-m minimum range restriction as the Criterion 400 is, so it was not necessary to ocularly distinguish between low vegetation hits or open sky hits. Additional data on the inclination angle of the Impulse instrument were recorded along with each height measurement. Because the instrument was pointed in a nearly vertical direction, we expected that these angles would all be nearly 90 degrees.

Estimation of foliage area profiles: MacArthur and Horn estimator

MacArthur and Horn (1969) derived an estimator for the leaf area index of a horizontal layer in the canopy as follows. Let \( D(h) \) denote the density of foliage at height \( h \) above the ground. Let \( \phi(h) \) denote the probability of a point quadrat passing through the lowest \( h \) metres without being intercepted. Denote a small increase in height above \( h \) as \( dh \). To compute the foliage area between any two heights \( h_1 < h_2 \), MacArthur and Horn (1969) integrated the foliage density function with respect to \( h \) over the interval \( h_1 \rightarrow h_2 \):

\[
L(h_1, h_2) = \int_{h_1}^{h_2} D(h) dh = \ln \frac{\phi(h_1)}{\phi(h_2)}
\]

where \( \phi(h) \) is estimated by the fraction of point quadrats that exceed \( h \), and all heights \( (h, h_1, h_2) \) are typically expressed in metres or fractions thereof. Because of the common normalizing denominator in \( \phi(h_1) \) and \( \phi(h_2) \) they arrived at the following estimator:

\[
L(h_1, h_2) = \ln \left( \frac{n_{h_2}}{n_{h_1}} \right)
\]

where \( n_{h_1} \) and \( n_{h_2} \) are the numbers of point quadrats whose height exceeded \( h_1 \) and \( h_2 \), respectively, \( n_{h_1} \geq n_{h_2} \).

Alternative estimator

An alternative estimator was derived based on the probability of point quadrats being intercepted within a horizontal layer in the canopy. The motivation for developing this estimator was to formalize the assumptions made in estimating foliage area by point quadrats, to frame the estimator within a statistical context, and for comparison with eq. 2. The canopy is divided into nonoverlapping horizontal layers (\( i = 1, 2, 3, \ldots \)) starting near the ground. For the set of point quadrats whose height exceeded the \( i \)th canopy layer, the proportional leaf area of layer \( i \) is the probability of interception of a point quadrat within that layer (assuming the leaves are not inclined away from the horizontal plane):

\[
p_i = \frac{x_i}{n_i}
\]

where \( x_i \) is the number of point-quadrat interceptions in layer \( i \) and \( n_i \) is the number of point-quadrat interceptions in and above layer \( i \) (including open sky hits).

Equation 3 relies on the assumption that there are no overlapping leaves within the \( i \)th layer. To guard against this assumption failing, we make the layer thickness as small as possible so as to reduce the possibility of overlapping of leaves. This is done by choosing a variable layer depth through the canopy so that exactly one point quadrat is intercepted within each layer. For such a thickness the foliage area of a layer is estimated as
between $h_1$ and $h_2$, eq. 4 is summed over the range of interest. This
the 18 field plots was 1495, with a range of 772-1981 (Ta-
the fraction
remains constant as the total number of point
 quadrats gets large: [7]
$$F(n_h) - F(n_{hi}) = \ln \left( \frac{n_{hi}}{n_h} \right) - \frac{1}{2} \left( \frac{n_{hi} - n_h}{n_h n_{hi}} \right) = \ln \left( \frac{n_{hi}}{n_h} \right)$$

The approximation should be good unless either $n_h$ or $n_{hi}$ is
small. Equation 7 provides a practical check of the magnitude of
difference between eqs. 2 and 5. Layer leaf area estimated from
eq. 5 is smaller only by a small factor from that estimated by eq. 2,
unless the number of point quadrats intercepted within a layer ($n_{hi} -
n_h$) is large relative to the product of $n_h$ and $n_{hi}$ (cf. eq. 7). Close
agreement between eqs. 2 and 5 is assured when the number of open
sky hits ($\kappa$) is large because all values of $n_h$ and $n_{hi}$ are larger than $\kappa$.

**Results**

The median number of laser point quadrats observed on
the 18 field plots was 1495, with a range of 772–1981 (Ta-
ble 1). Variation in the number of point quadrats was due to
minor differences in plot and grid sizes at different sample
locations. The median number of recorded sky hits was 35.5,
with values ranging between 9 and 88 over the 18 field
plots. Collection times ranged between 1.5 and 2.5 h per
field plot, excluding travel time. For some plots, heavy
understory vegetation caused a relatively large number of
point-quadrat interceptions within 3 m above the Criterion
400 unit (Table 1). In conditions where upper canopy foliage
was sparse above a moderately dense layer of low vegeta-
tion, it was somewhat difficult to precisely distinguish be-
tween low hits and open sky hits.

**Total LAI**

Total LAI for each plot was estimated from eq. 2 as the
natural logarithm of the ratio of point quadrats taken ($n$) to $\kappa$
(Table 1, column 6). The ratio $n_h$ is equivalent to the recip-
rocal of the gap fraction ($g$), where $g$ is defined as the frac-
tion of the plot ground area covered by any gap in live
vegetation. The LAI estimates based on gap fraction showed
no significant correlation with litter fall LAI obtained from
earlier studies (Vose et al. 1995; Bolstad et al. 2001) at the
same sites (Table 1, column 5) ($r^2 = 0.03, p = 0.49$). Because
relatively large numbers of sky hits were observed (more
than nine), the estimators (eqs. 2 and 5) gave nearly identical
results so only one set of laser point-quadrat LAI estimates
is listed in Table 1.

**Foliage area profiles**

Canopy profiles were obtained using the estimator in eq. 5
dividing the canopy into horizontal layers of 1 m (Fig. 1).
The 1-m layer thickness was chosen to facilitate comparison
with the data of Vose et al. (1995). To further facilitate com-
parison with their data, the laser point-quadrat based layer
leaf areas were multiplied by a constant so that their sums
would equal the sums of layer leaf areas observed by Vose et

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**Table 1. Summary of sampling effort and comparison of total LAI estimates with litter fall LAI for 18 laser point-quadrat field plots.**

<table>
<thead>
<tr>
<th>Plot</th>
<th>Point quadrats</th>
<th>Sky hits</th>
<th>Low hits</th>
<th>Litter fall LAI</th>
<th>Laser point-quadrat LAI</th>
</tr>
</thead>
<tbody>
<tr>
<td>W2 low</td>
<td>1149</td>
<td>62</td>
<td>418</td>
<td>4.3</td>
<td>2.92</td>
</tr>
<tr>
<td>W2 high</td>
<td>1758</td>
<td>28</td>
<td>501</td>
<td>4.5</td>
<td>4.14</td>
</tr>
<tr>
<td>W27 low</td>
<td>1511</td>
<td>28</td>
<td>570</td>
<td>4.7</td>
<td>4.09</td>
</tr>
<tr>
<td>W27 high</td>
<td>1319</td>
<td>18</td>
<td>500</td>
<td>5.4</td>
<td>4.29</td>
</tr>
<tr>
<td>A</td>
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<td>22</td>
<td>766</td>
<td>4.59</td>
<td>4.44</td>
</tr>
<tr>
<td>B</td>
<td>1358</td>
<td>62</td>
<td>348</td>
<td>6.42</td>
<td>3.09</td>
</tr>
<tr>
<td>C</td>
<td>1222</td>
<td>56</td>
<td>430</td>
<td>2.63</td>
<td>3.08</td>
</tr>
<tr>
<td>D</td>
<td>1981</td>
<td>12</td>
<td>285</td>
<td>5.11</td>
<td>5.11</td>
</tr>
<tr>
<td>E</td>
<td>1548</td>
<td>57</td>
<td>555</td>
<td>6.37</td>
<td>3.30</td>
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<tr>
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<tr>
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<td>88</td>
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<td>2.85</td>
</tr>
</tbody>
</table>

Note: Litter fall data are from Vose et al. (1995), Bolstad et al. (2001), and Bolstad (unpublished data). Plot codes are used in Figs. 1–4.
Cumulative LAI profiles

Data obtained from laser point quadrats are well suited for development of cumulative foliage profiles (CFPs). The CFP is another way to express foliage-height profiles that is often useful in modeling applications (e.g., Ellsworth and Reich 1993; Yang et al. 1999). Because point-quadrat intercept heights are recorded on a continuous scale, relatively smooth CFPs can be developed (Fig. 4). CFPs are often normalized between 0 and 1 to facilitate modeling by cumulative density functions and for statistical comparisons involving Kolmogorov–Smirnov (KS) two sample or goodness-of-fit tests (Lindgren 1993). A layer is centered at each height where one or more laser point quadrats were intercepted. The layer leaf area is estimated by eq. 2 or 5 and accumulated from the top of the canopy downward, as is customary for CFPs (Fig. 4). Numerical differences between the two estimators, although greatest at the top of the canopy,
are too small to be perceived in plots like those shown in Fig. 4.

The KS two-sample test statistic (Lindgren 1993) was computed to compare canopy profiles from Vose et al. (1995) with the profiles developed from laser point quadrats. Test statistics were computed based on the greatest absolute difference between the two CFPs being compared. For watershed 2 low a maximum difference of 0.21 between CFPs was observed corresponding to a canopy height of 10 m ($p = 0.44$). For watershed 2 high a maximum difference of 0.28 was observed between CFPs, corresponding to a canopy height of 15 m ($p = 0.21$). The maximum difference observed in comparing either of the watershed 27 CFPs was 0.12, corresponding to a canopy height of 18 m at watershed 27 low ($p > 0.5$).

The CFPs developed from this technique were nearly continuous over the sampled vertical ranges of the canopies studied. To examine patterns of continuity in the foliage profiles, the distance between consecutive laser intercept heights was denoted $Z$. Note that $Z$ corresponds to the thickness of the layers for which LAI would be estimated using eq. 4. The average $Z$ values for the 18 field plots studied were typically between 2 and 3 cm. The median $Z$ values were either 1 or 2 cm. The largest $Z$ values were observed at the lowest and highest canopy heights. Often, one or two laser point quadrats were intercepted at a distance considerably higher than any other intercept. For example, this was the case for one point quadrat on plot B intercepted at 24.5 m ($Z = 2.1$ m) (cf. Fig. 4).

**Laser point-quadrat inclination**

To verify the vertical orientation of point quadrats, data on laser point-quadrat inclination were collected along with interception heights on field plot 16 at Cedar Creek. Of the 1460
point quadrats intercepted in the canopy, the mean point-quadrat inclination was 89.5° with a standard deviation of 3.1°. Based on visual inspection and a KS goodness-of-fit test (Lindgren 1993), the distribution of point-quadrat inclination angles was not obviously different from a normal distribution with the same mean and standard deviation (p = 0.09).

Discussion

Plant area index (PAI)

Interceptions with both wood and foliage tissue are possible, so that all the results presented here technically refer to PAI, not LAI. This is the case for many of the indirect sampling methods we reviewed. An adjustment could be obtained by visiting the field plot during the leafless season and estimating the projected area of leafless tissue with laser point quadrats. Use of a visible laser might also aid in distinguishing between leaf and wood interceptions. For sampling methods that involve manual determination of point-quadrat interceptions (i.e., optical point-quadrat sampling), non-leaf interceptions can be partitioned if the primary interest is LAI. Little attention has been paid to this detail in published studies, although Denison and Russotti (1997) used laser-induced chlorophyll fluorescence to estimate the area of green leaf tissue in row crops.

Total LAI

Laser point-quadrat sampling offers no obvious improvement over optical point-quadrat sampling for estimating total LAI. Neither technique appears useful for estimating total LAI (cf. Aber 1979b). The apparent failure of these techniques is due to violations of one or more assumptions made in estimating total LAI. Various assumptions were made, and those that may have been violated include (i) zero leaf-inclination; (ii) error-free classification of sky hits versus low hits; (iii) negligible cross-sectional area of the laser point quadrat; (iv) adequately large sample sizes; (v) random spatial distribution of leaves within canopy layers; and (vi) independence of the spatial distributions between canopy layers.

Errors due to leaf inclination (the first assumption) can be addressed by the use of inclined point quadrats (Warren Wilson and Reeve 1963; Denison 1997) or an estimator that accounts for inclination angles. Field data from this study showed that point-quadrat inclination angles differed only slightly from vertical. Inclined laser point-quadrat sampling could easily be conducted with hand-held laser range finders, but correction for inclination angles essentially involves the adjustment of vertical point-quadrat based LAI estimates by a multiplicative constant. This correction would not remedy the complete lack of a trend between indirectly observed LAI and estimates from litter fall found here. Following the method of Warren Wilson and Reeve (1963), it should be possible to estimate leaf inclination angles at different heights in the canopy with laser point quadrats; however, this was not attempted here.

The need to ocularly distinguish between low canopy hits and open sky hits was a potential source of error because of misclassification of open sky hits (the second assumption). This error source was due only to the minimum range limita-

tion of the Criterion 400. It is not an inherent weakness of the laser point-quadrat method. It can readily be overcome by using an instrument with no minimum range limitation, such as the Impulse. Use of a visible laser might also aid in distinguishing between low canopy hits and sky hits. It was not possible to ascertain the magnitude of misclassification errors from the data collected in this study.

When the point quadrat or probe used to measure leaf interceptions has an appreciable cross-sectional area, a bias in foliage area estimation occurs (the third assumption) (Warren Wilson 1963). The bias increases as point-quadrat thickness increases. Here, an important weakness of the laser point-quadrat technique is realized. Laser-beam divergence causes point-quadrat thickness to increase as the beam penetrates higher into the canopy, so the bias is proportional to the canopy height. It may be possible to account for beam thickness by adjustment of the foliage area estimator, but additional assumptions about leaf sizes and shapes would be required. Another solution would be to use a laser with a very narrow divergence.

Related to the problem of beam thickness is the issue of errors resulting from the processes of reflection that cause a point-quadrat interception to be recorded by the instrument. For instance, it is not known whether the sensitivity of the instrument to detect any foliage tissue decreases with the distance to point of interception. Little information was available regarding the properties of beam reflectance that determine whether and where a laser point-quadrat is intercepted by plant material in the canopy. Assessment of other factors that might cause measurement errors, e.g., slight movement of the laser instrument during sampling or movement of foliage due to wind, was not carried out. A further development of the laser point-quadrat technique would include the characterization of how beam reflectance properties or errors due to instrument and foliage movement might affect the accuracy of the estimated foliage profiles.

Underestimation of total LAI will occur if too few sample point quadrats are taken (the fourth assumption) (Aber 1979b). The maximum observable LAI from estimators eqs. 2 and 5 is limited by the ratio of sample point quadrats taken per open sky hit (1/γ). Inverting eq. 2 gives the gap fraction corresponding to a particular LAI. For example, the largest LAI observed from litter fall data on the field plots in this study (6.4) corresponds to a gap fraction of e^{-0.0017}. Observation of this gap fraction requires a ratio of roughly 600 laser point quadrats for every sky hit. The need for large samples is evident when LAI is large. Any errors in classifying point quadrats (low hits vs. sky hits) could have considerable effects on estimates of the gap fraction, especially when the actual gap fraction is small. Here, large samples of laser point quadrats were obtained with a practical amount of effort, but the relatively large sample sizes did not lead to a satisfactory agreement between litter fall and laser point-quadrat estimates of LAI.

Perhaps the most serious problems with the technique are related to the nonrandom positioning of leaves and the lack of independence of leaf positions within and between horizontal layers (the fifth and sixth assumptions). Between-layer correlation in leaf positions can seriously affect total LAI estimates. Any between-layer spatial correlations that affect the gap fraction will distort estimates of total LAI.
Problems related to nonrandomness of the spatial distribution of foliage are well known and have been discussed in published reviews of canopy structure measurement techniques (e.g., Welles and Cohen 1996).

Foliage area profiles

The foliage profiles developed here for hardwood forests in central Minnesota and western North Carolina (Figs. 1-3) appear plausible when compared with other published profiles for broadleaf deciduous species (Miller 1967; Ford and Newbould 1971; Aber 1979a, 1979b; Jurik et al. 1985; Hutchison et al. 1986; Hedman and Binkley 1988; Chason et al. 1991; Wang et al. 1992; Yang et al. 1993; Ellsworth and Reich 1993; Strachan and McCaughey 1996; Raulier and Ung 1997; Tanaka et al. 1998; Lefsky et al. 1999; Yang et al. 1999). Large samples of laser point quadrats can be obtained relatively quickly and handled electronically, minimizing errors that might occur because of small sample sizes or manual data recording. The laser point-quadrat technique appears to offer a promising alternative to other direct and indirect sampling methods for estimation of vertical foliage area profiles; however, additional testing should be carried out.

Results of Aber (1979b) supported the hypothesis that foliage profiles taken with optical point quadrats agreed with those derived using plumb lines or other mechanical point quadrats. Here laser point-quadrat results and the canopy profiles obtained with plumb lines by Vose et al. (1995) were visibly dissimilar for watershed 2 field plots. In contrast, watershed 27 profiles were noticeably alike (Fig. 1). Although the two-sample KS test indicated no significant difference between plumb line and laser point-quadrat CFPs for any of these four field plots, this test was found to have little practical ability to detect such a difference. Formally rejecting the null hypothesis of a common foliage profile would require a rather large difference between the two CFPs, even with a modest control on type I error ($\alpha = 0.1$), of over 32% of accumulated LAI at a given height. Because these data are not based on counted point-quadrat interceptions in each canopy stratum, standard contingency table analysis (Lindgren 1993) does not provide a means for comparison. Further research might investigate the availability of significance tests for comparing foliage profiles from laser point quadrats with those obtained using mechanical point-intercept techniques.

One factor that would contribute to differences between the results of the two studies is the difference in sampling intensity and the spatial variability of sample point quadrats for the two methods. The potential for this type of error seems quite high, especially in light of the limited number (six) of plumb lines used in the previous study and their proximity to a narrow canopy tower. The Coweeta watershed 2 plumb line profiles are quite disjoint (Fig. 4) in comparison with foliage-height profiles typically observed in broad-leaved canopies, which are generally considered to be smooth and continuous (e.g., Yang et al. 1999). Because the large samples of laser point quadrats allowed for the development of relatively smooth foliage-height profiles, the laser data may give a more accurate representation of the actual canopy structure than plumb line data.

Another factor that would contribute to differences between the two studies is the change in canopy structure over time. Although no independent data were collected to assess the degree of change in canopy structure since 1993, the year Vose et al. (1995) collected their data, some change must be assumed. Given the likelihood of change in canopy structure over a 6-year period, and the different sampling intensity of the two methods compared, it is difficult to make an objective assessment of the accuracy of foliage-height profiles developed from either of these two techniques. Still, it seems promising that the laser profiles visually match the plumb line results for watershed 27.

Conclusions

Laser point quadrats provide an attractive alternative to optical point quadrats or other indirect sampling methods used to estimate foliage-height profiles in broad-leaved forests. Large samples can be collected within a relatively short amount of time under normal field conditions. The ability to store data on a field computer facilitates analysis and reduces the possibility of certain measurement errors. In addition, laser point-quadrat measurements are reportedly accurate to within a few centimetres. Data from laser point quadrats can be used to develop foliage-height profiles or cumulative foliage profiles. The technique is apparently not useful for estimating total LAI, as is the case for other indirect sampling methods presently in use.

An alternative to the estimator of (MacArthur and Horn 1969) for determining foliage-height profiles was developed based on the probability of point quadrats being intercepted within a horizontal layer in the canopy. The two estimators gave nearly identical results when large numbers of point quadrats were taken. The alternative estimator included a term in its formula that showed how the two estimators gave divergent results when the sample size was small, specifically, as the number of open sky hits was small.

Future research should be conducted to test the accuracy of foliage-height profiles developed by laser point quadrats. Ideally, a large set of independent profiles should be compared with profiles obtained by laser point quadrats. A more powerful test for comparing profiles from alternative methods is needed. Studies using inclined point quadrats should be conducted to correct for errors due to leaf inclination changes through the canopy. Finally, significant efforts should be made to determine how robust the estimates are to violations of the stated assumptions, and to mitigate any serious effects of violations. Such efforts would investigate how the method of determining foliage-height profiles is affected by the reflective properties of foliage, laser beam divergence, movement of the laser instrument or the leaves, and nonrandomness or between-layer correlation in the spatial orientation of leaves.

Acknowledgements

This study was supported by USDA Forest Service, Southern Global Climate Change Program, the National Science Foundation Coweeta Long-Term Ecological Research Project, and the University of Minnesota Agricultural Exper-
The authors thank Graham W. Mahal and Jonathan G. Martin for help with data collection.

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