Estimating Oak Leaf Area Index and Gypsy Moth, 
Lymantria dispar (L.) (Lepidoptera: Lymantriidae), 
Defoliation Using Canopy Photographs

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ABSTRACT Oak leaf area index (LAI) was estimated using wide-angle photographs of the forest canopy taken from the ground at grid points throughout three sites on Cape Cod, Mass. Confidence intervals for these estimates and optimal sample sizes were calculated. Oak LAI estimates leveled off by early June when no defoliation was present. Within-plot two-dimensional spatial distribution of oak LAI was very similar to the spatial distribution of oak basal area. Consequently, there was a positive correlation between local oak leaf area and local basal area. Comparison of LAI estimates taken before and after gypsy moth, Lymantria dispar (L.), defoliation allowed the estimation of oak leaf area consumed. Leaf area loss was similar in areas of high and low host foliage densities. The correlation of leaf area lost with local density of early instars was greater than the correlation with the density of late instars.

KEY WORDS Insecta, damage, impact, sampling

Many hardwood forests in the northeastern United States are defoliated when gypsy moth, Lymantria dispar L., populations occasionally reach outbreak densities. Area-wide defoliation is routinely estimated using aerial sketch mapping and photometric interpretation (Talerico 1981). However, current methods to quantify the intensity and within-stand variation in defoliation are crude. Most previous studies have relied on visual estimation of relative defoliation rather than actual quantification of the foliage removed (Connola et al. 1966, Talerico 1981).

Several strategies are available for estimating forest tree foliage density. The simplest approach is to sample leaf populations and measure or estimate individual leaf biomass or area (Sestak et al. 1971, Reichle et al. 1973). Direct measurement of foliage density is labor-intensive. Foliage area can more easily be estimated from indirect measurements, such as from measurements of litterfall (Marshall & Waring 1986), tree branch or petiole girth (Kittredge 1944, Rothacher et al. 1954, Attiwill 1962, Linit et al. 1986), sapwood basal area (Grier & Waring 1974, Rogers & Hinckley 1979, Marshall & Waring 1986), and from measurements of light interception (Leong et al. 1982, Marshall & Waring 1986). Except for the last-named technique, these methods do not lend themselves to estimation of defoliation. However, it is possible to use light interception estimates taken before and after defoliation to estimate leaf area consumed. Other measures of foliage quantity, such as biomass, can be estimated easily from leaf area estimates (Sestak et al. 1971).

Wang & Miller (1987) described a method for estimating the leaf area index (LAI) of oak forests using vertical hemispherical photographs (LAI is the area of foliar surface per unit of soil surface area); temperate forest stands have values as high as 12 (Kira 1975). In this study, we used this technique to measure LAI at three sites on Cape Cod, Mass. By measuring LAI before and after gypsy moth defoliation, we were able to estimate the leaf area that was consumed. These data were also used to develop sampling guidelines for making these estimates.

Materials and Methods

Oak LAI was estimated at two 9-ha plots and one 16-ha plot in 1985 on Otis Airforce Base, Cape Cod, Mass. These plots were composed almost entirely of pitch pine, Pinus rigida Mill., small-diameter black oak, Quercus velutina Lam., and white oak, Q. alba L. The top of the oak canopy was approximately 8 m at all plots. Estimates were made in all three plots in late June when oak shoots were fully elongated but before noticeable defoliation had occurred. At one site (Plot 2), oak LAI was also estimated in late July, when defoliation was at its peak. At the other two sites, gypsy moth densities were low and no defoliation occurred; a second estimate was not taken.

Within each 9-ha plot, a grid (13 x 13) with 25 m between grid points was surveyed, and a grid (5 x 17) with 50 m between grid points was located at the 16-ha plot. At each grid point, a photograph...
Table 1. Mean LAI estimates, standard errors, and optimal sample sizes

<table>
<thead>
<tr>
<th>Plot</th>
<th>(P^*)</th>
<th>(P)</th>
<th>(s^2_1)</th>
<th>(s^2_2)</th>
<th>LAI</th>
<th>SE</th>
<th>(J_{opt})</th>
<th>(P^{1/20})</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>364</td>
<td>169</td>
<td>0.43</td>
<td>0.20</td>
<td>1.91</td>
<td>0.08</td>
<td>2</td>
<td>28</td>
</tr>
<tr>
<td>2a</td>
<td>364</td>
<td>169</td>
<td>0.31</td>
<td>0.22</td>
<td>1.99</td>
<td>0.07</td>
<td>3</td>
<td>26</td>
</tr>
<tr>
<td>2b</td>
<td>364</td>
<td>169</td>
<td>0.28</td>
<td>0.27</td>
<td>1.09</td>
<td>0.07</td>
<td>3</td>
<td>26</td>
</tr>
<tr>
<td>3</td>
<td>467</td>
<td>86</td>
<td>0.58</td>
<td>0.20</td>
<td>1.35</td>
<td>0.17</td>
<td>2</td>
<td>56</td>
</tr>
</tbody>
</table>

\(P\), number of photographs in sample; \(P^*\), total number of nonoverlapping photographs possible in plot; \(s^2_1\), among-photograph variance; \(s^2_2\), among-circle variance; LAI, LAI estimate; SE, standard error of estimate; \(J_{opt}\), optimal number of circles per photograph; \(P^{1/20}\), number of photographs necessary to obtain an estimate within 20% of the true mean.

* No defoliation.

Was taken from 35-mm film. Each photograph was projected onto a circular grid on a white surface (1 by 1.5 m). This circular grid consisted of nine concentric circles calculated to subtend angles of 5, 15, 25, 35, 45, 55, 65, 75, and 85°. 108 grid points were located at the intersections of these nine circles with 12 lines radiating from the center. Of these points, 14 could not be used because they fell off the photograph. At each of the remaining grid points, it was determined if the photograph projected on the point was oak leaf, pine foliage, a branch, or sky. For each concentric circle (angle) a gap frequency (G) was calculated:

\[
G = \frac{\text{points that fell on sky + points that fell on pine foliage}}{\text{number of points that did not fall on branches}}
\]

Points that fell on branches were excluded from the calculation of G, because it was unknown whether a leaf or sky was behind the branch. We did not attempt to measure the pine LAI. Therefore, points that fell on pine foliage were considered equivalent to points that fell on sky, because pine foliage was largely above the oak canopy.

Wang & Miller’s (1987) estimator of LAI was:

\[
\text{LAI} = \frac{1}{J} \sum_{j=1}^{J} \frac{1}{(1/\mu_j) \ln(G_j)}
\]

in which \(j\) is consecutive angles of concentric circles, \(J\) is the number of concentric circles per photograph, and \(\mu_j\) is the extinction coefficient.

The extinction coefficient is a parameter of the Lambert–Beer law (Wang & Miller 1987) and is a relative measure of the interception of light passing through the forest canopy for a given LAI. This parameter is specific to the elevation angle of the light source and is a function of the leaf-angle distribution. Extinction coefficients in deciduous forests typically vary between 0.4 and 0.5 (Kira et al. 1969). Wang (1985) found that in a stand (Plot 2) on Cape Cod, the extinction coefficients for angles of 40–90° above the horizon were essentially constant at 0.46, but below 40° (as the angle approached the horizon) \(\mu_j\) approached infinity. Wang (1985) used a 110° fish-eye lens (35° above the horizon). The lens used in the present study subtended only 85° (47.5° above the horizon); hence, in this canopy \(j\) was within the range where \(\mu_j\) was approximately constant. Thus Equation 2 reduced to:

\[
\text{LAI} = \frac{1}{(0.46J)} \sum_{j=1}^{J} [-\ln(G_j)].
\]

The among-photographs variance was calculated by:

\[
s^2_1 = \left(\frac{1}{0.46}\right)^2 \sum_{p=1}^{P} \left[\frac{\left(\ln(G)\right)_p - \left(\ln(G)\right)}{p - 1}\right]^2
\]

in which \(s^2_1\) is the sample variance among photograph means, \((\ln(G))_p\) is the mean of the \(J\) \((\ln(G))_j\) of photograph \(p\), and \((\ln(G))\) is the mean of the \(P\) \((\ln(G))_j\) for the whole plot.

The among-circles sample variance was calculated by:

\[
s^2_2 = \left(\frac{1}{0.46}\right)^2 \sum_{p=1}^{P} \sum_{j=1}^{J} \left[\frac{\left(\ln(G)\right)_p - \left(\ln(G)\right)}{P(J - 1)}\right]^2
\]

in which \(s^2_2\) is the sample variance among circles within photographs.

In estimating the total variance, the total number of photographs was sampled, many of which could be taken within a forest, represent a special case of cluster sampling (Cochran 1977), in which photographs represent clusters and an infinite number of circles could be sampled from each photograph. Thus, the variance of LAI, \((s^2_r)\) can be estimated by:

\[
s^2_r = \frac{P^* - P}{P \cdot P^*} s^2_1 + \frac{s^2_2}{P^* J}
\]
Table 2. Spearman rank correlation coefficients between estimated oak LAI and oak basal area; basal area was measured within circles about each grid point.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Basal area, circle diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4 m</td>
</tr>
<tr>
<td>1</td>
<td>0.562</td>
</tr>
<tr>
<td>2</td>
<td>0.496</td>
</tr>
<tr>
<td>3</td>
<td>0.619</td>
</tr>
</tbody>
</table>

The spatial patterns of oak LAI and defoliation were graphically displayed using the Surface-II graphics program (Sampson 1978). A grid (25 × 25) was generated from the grid (13 × 13) of LAI estimates at each point in the stand. The new grid points were calculated as the weighted mean of the closest eight sample grid points. Scaled inverse distance squared was used for the weighting function. Contour lines were smoothed using a piecewise Bessel interpolation.

The relationship between oak basal area and estimated oak LAI was studied by measuring the diameters of all trees >3 cm diameter at breast height (dbh) within 5 m of each grid point. In addition, the distance from the grid point was measured for each tree. A Spearman rank correlation coefficient (Sokal & Rohlf 1981) was calculated between estimated oak LAI and basal area at each sample grid point. Separate correlation coefficients were calculated for basal area in 10-, 7-, and 4-m diameters around the grid point. Separate correlations were performed for each of the three sites.

The relationship of leaf area defoliated (oak LAI before defoliation − LAI after defoliation) to local larval density was studied by measuring frass drop at each station where LAI was estimated. Conical frass traps (Liebhold & Elkinton 1988a,b) were deployed at each point where canopy photographs were taken. Simultaneous estimation of frass drop (amount of frass falling from the canopy per unit forest area) and frass yield (amount of frass produced per larva [Liebhold & Elkinton 1988a,b]) during a 12-h interval allowed estimation of the density of larvae above each frass trap at each point. These estimates were made on four occasions from late May, when third instars predominated, to late June, when fifth instars predominated. The correlation between defoliation and gypsy moth density was evaluated for each of the larval sampling periods.

The temporal distribution of LAI (without defoliation) was studied by taking LAI estimates on five occasions from the time of bud break in early May through August 1986, when no defoliation occurred at these plots. On each occasion, canopy photographs were taken at five points at Plot 1 and at Plot 2. The mean LAI at each plot were compared between occasions using a two-way analysis of variance in which the effects were occasion, point, and the occasion–point interaction. Means
were compared using Tukey’s HSD (Sokal & Rohlf 1981).

Results and Discussion

Oak LAI estimates at the three plots ranged from 1.0 to 2.0 (Table 1). Oak LAI at Plots 1 and 2 were slightly greater than at Plot 3. These LAI are low compared with total LAI estimates from other temperate forests (Kira 1975). This difference is most likely a result of poor site conditions, young age of these stands, and an unmeasured proportion of the canopy occupied by pitch pine.

At all four measurements, the sample variance among photographs ($s^2_\gamma$) was greater than the sample variance among circles ($s^2_\circ$) (Table 1). This reflects the nature of the distribution of foliage within these stands; foliage is aggregated as trees and also as groups of trees. Within each plot, foliage appears to be spatially aggregated (Fig. 1A, 2A and B).
Spatial variation was greatest at Plot 3, probably because of the presence of several depressions that lack large oak stems.

The cost per canopy photograph replicate, not including overhead, was $0.67 ($0.20 film, $0.12 processing, $0.35 labor). The cost of transcribing a set of data from a circle on a slide and entering the data was $0.08 per circle (for labor).

Given the magnitude of the among-photograph and among-circle sample variances and the relative magnitudes of the costs, the optimal number of circles per photograph for estimating oak LAI in Cape Cod forests (in terms of minimizing the variance) was two or three (Table 1). Thus, even though it is much less expensive to replicate the number of circles within a photograph, it is better to take more photographs, because the among-photograph variance is much greater than the among-circle variance. Between 20 and 80 photographs may be required to estimate the spatially averaged oak LAI with a confidence interval that is within 20% of the mean 95% of the time (Table 1). When the among-photograph variance is high (such as at Plot 3), a larger number of samples are necessary (Equation 9). If LAI is estimated over a smaller area, the among-photograph variance will usually be low; consequently the number of required samples will be lower. Also, if the LAI to be estimated is low (such as at Plot 2 after defoliation), a large number of samples will be required. Optimal allocations of samples are probably different when angles closer to the horizon are sampled because of the nonlinearity of $\mu_i$ and $G_i$ as the path lengths through the canopy increase.

The spatial patterns of oak leaf area (Fig. 1A) were very similar to those of oak basal area (Fig. 1B). At all three sites, LAI estimates (taken before defoliation) were significantly correlated with local basal area measurements (Table 2). Correlations were consistently higher for basal area measurements within a 7- and 10-m-diameter circle about each point than they were for basal area measurements restricted to a 4-m-diameter circle. The volume sampled by a canopy photograph is an inverted cone (Fig. 3A). Presumably, if basal area measurements are restricted within a very small radius, the basal area would not be measured for trees that are outside the circle but whose crowns are within the cone (Fig. 3B). Conversely, if basal area is measured in a large radius about each point, trees will be measured even though their crowns are outside of the cone. Thus, there is undoubtedly some radius from the center where a maximal correlation occurs. This distance will be longer in stands where trees are taller. Rogers & Hinckley (1979) found that current sapwood area was a better predictor of oak leaf area than was total stem area.

At Plot 2 in 1985, there was a significant drop in oak LAI from the June measurement (before defoliation) to the late July measurement (peak defoliation) (Table 1, Fig. 2A–C). Approximately 45% of the oak foliage in the stand was removed by gypsy moth feeding. The amount of foliage removed appeared to be linearly related to the initial amount of foliage at each point, although there was considerable variation about this relationship (Fig. 4). The linearity of this function indicated that defoliation was not intensified in areas of high host foliage; instead, a relatively fixed pro-
portion of foliage was removed at all host foliage densities.

The correlations of leaf area defoliated with larval density were significant for all four larval density estimates, although the correlation coefficients were generally low on all occasions (Fig. 5, Table 3). Both the defoliation and density estimates have errors associated with them; these may contribute to the "noise" about this relationship. Also, the defoliation estimates and density estimates are probably drawn from slightly different volumes of the canopy; this may also contribute noise. Correlations were not consistently different among the three levels of resolution (Table 3). However, the correlation seemed to be greater early in the season than late in the season. The correlation of larval density with local host foliage density decreased through larval development (Liebhold & Elkinton, unpublished data); most likely this is caused by larvae moving from their favored hosts (oaks) to less preferred hosts (pines) during the later stadia (Lance & Barbosa 1982, Wallner 1983, Rossiter 1987). Probably this movement onto less-preferred hosts caused the decrease in the correlation of density with oak defoliation. During the late stadia, many larvae may have been feeding in pines; their densities would be measured from frass drop, but their defoliating impact would not be measured using our technique.

Estimates of LAI on successive occasions from oak bud break in early May through August indicated that by early June, LAI had reached a plateau (Fig. 6). This indicates that before-defoliation LAI estimates may be taken in early June and safely compared with peak-defoliation LAI estimates to determine defoliation LAI. The timing of defoliation will differ among various regions; thus the timing of photographs should be specific to the phenology of local populations.

We expect that it would be difficult to differentiate oak leaves from other hardwood species when transcribing data from slides. Furthermore, extinction coefficients have not been determined for other species in other stands. Under these circumstances, it may be possible to measure a dif-

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**Table 3. Spearman rank correlations between larval density (as measured by frass drop) and defoliation (LAI before defoliation - LAI after defoliation) at three levels of spatial scale**

<table>
<thead>
<tr>
<th>Date</th>
<th>Correlation coefficients</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>169 grid points&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>30 May</td>
<td>0.544&lt;sup&gt;*&lt;/sup&gt;</td>
</tr>
<tr>
<td>8 June</td>
<td>0.550&lt;sup&gt;*&lt;/sup&gt;</td>
</tr>
<tr>
<td>13 June</td>
<td>0.375&lt;sup&gt;*&lt;/sup&gt;</td>
</tr>
<tr>
<td>20 June</td>
<td>0.417&lt;sup&gt;*&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup> correlation coefficient significantly greater than 0 (P ≤ 0.01).

<sup>b</sup> Paired density and defoliation measurements represent single observations from individual grid points (n = 169).

<sup>c</sup> Paired density and defoliation measurements represent means of all grid points falling inside of 0.25-ha subplots (n = 36).

<sup>d</sup> Paired density and defoliation measurements represent means of all grid points falling inside of 1-ha subplots (n = 9).
ference in total (not oak alone) leaf area using direct measurements of solar radiation rather than light interception (Marshall & Waring 1986), or to measure a difference in relative canopy density (Cooper et al. 1987; C. G. Jones & M. J. Fargione, personal communication).

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