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Performance of the LAI-2000 plant canopy analyzer in estimating leaf area index of some Scots pine stands

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Summary

The LAI-2000 plant canopy analyzer (Li-Cor, Inc., Lincoln, NE) was tested at six experimental plots of Scots pine (*Pinus sylvestris* L.) in central Sweden at peak leaf area in August and after litterfall in October 1990. An independent estimate of leaf area index for August 1990 was obtained based on an empirically derived regression of needle area on stem sapwood area, and the decrease in leaf area between the two measurements was estimated from measurements of litterfall.

A strong linear relationship was found between estimates by the LAI-2000 ($L^{\text{Li-Cor}}$) and the indirect estimates of leaf area index (taken as half of total surface area) (L). The finding that $L^{\text{Li-Cor}}$ was considerably smaller than L was explained theoretically. It was shown that if shoots, instead of individual needles, are randomly distributed in the canopy, $L^{\text{Li-Cor}}$ corresponds to L multiplied by a factor (β) characterizing the mutual shading of needles on the shoot. The shading factor, β, was equal to the ratio of spherically projected shoot area to spherically projected needle area, where the spherically projected area is defined as the average projection (silhouette) area taken over all directions in space. The quantity βL was defined as the shoot silhouette area index (SSAI), and an equation for the relationship between SSAI and the mean silhouette to total area ratio ($\overline{\text{STAR}}$) of shoots was derived.

Measured values of $\overline{\text{STAR}}$ for Scots pine indicated that $L^{\text{Li-Cor}}$ corresponds to SSAI rather than L. However, the decrease in leaf area index due to litterfall occurring between August and October was only partly detected by the LAI-2000, possibly because SSAI did not change to the same degree as L, i.e., there was an increase in the factor β. This hypothesis is supported by data showing a large increase in $\overline{\text{STAR}}$ with shoot age.

Keywords: canopy transmittance, shoot silhouette area index, STAR.

Introduction

Indirect estimates of leaf area index made by radiative techniques, such as different line quantum sensors, the DEMON (CSIRO, Canberra, Australia) and the LAI-2000 plant canopy analyzer (Li-Cor, Inc., Lincoln, NE), rely on the strong dependency between canopy structure and gap fraction of the canopy (e.g., Lang 1986, Welles 1990). The gap fraction of a canopy is the fraction of view in some direction from beneath the canopy that is not blocked by foliage, and it corresponds approximately to the transmittance of radiation in those wavelengths of radiation where scattering by foliage is small.

In all of these methods, the inversion of gap fraction data to estimates of leaf area index is based on Beer's law as applied to leaf canopies, with the assumption that the locations of leaves are statistically independent random variables with a uniform density function in the canopy (i.e., leaves are randomly distributed). Beer's law states that the penetration of direct light is described by a negative-exponential function of leaf area density integrated along the path of the solar beam within the canopy. Further, the extinction coefficient for flat leaves in this function is equal to the ratio of projected to one-sided leaf area (the mean projection of unit foliage area, see Nilson 1971).

The structure of a coniferous forest differs in two important respects from the homogeneous broad-leaved canopies for which the theory of inversion from canopy gap fraction to leaf area index was derived. First, because needles are not flat, the meaning of one-sided leaf area is unclear and equations derived for the extinction coefficient (the ratio of projected to one-sided leaf area) cannot be applied. Second, the grouping of needles into shoots and branches invalidates the assumption of randomly located leaves (needles). Because grouping (clumping) increases the canopy gap fraction at a given leaf area, indirect methods such as the LAI-2000 give estimates of an effective leaf area index, which is smaller than the actual leaf area index (Chen et al. 1991, Chason et al. 1991). For example, in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Smith et al. (1993) found that the LAI-2000 underestimated leaf area by 62%, i.e., the effective leaf area index was only 38% of the actual leaf area.

Beer's law equation can be modified to hold true in canopies if shoots instead of leaves (needles) are assumed to be randomly distributed (Stenberg et al. 1994). Under this assumption, the extinction coefficient represents the ratio of shoot silhouette area to needle area, and the inversion of gap fraction data by indirect methods such as the LAI-2000 yields an estimate of shoot silhouette area. The hypothesis that the LAI-2000 gives an estimate of shoot silhouette area rather than projected needle area was tested on four conifer species by Gower and Norman (1991). They found good agreement between direct estimates of (projected) leaf area index and LAI-2000 estimates multiplied by an empirical correction factor representing the ratio of projected needle area to shoot silhouette area in each of the species. However, the correction factor was not defined on a theoretically sound basis because it did not account for the variation in shoot silhouette area as a function of shoot orientation and direction of radiation. Thus, although their results supported their hypothesis, the correction factors were not adequately estimated.

The aim of this study was to test the LAI-2000 plant canopy analyzer in Scots pine (*Pinus sylvestris* L.) stands, and to analyze the effect of grouping needles into shoots on the estimates of leaf area index. Estimates obtained by the LAI-2000 were compared to (1) independent estimates of leaf area index (L) from regression of needle area on stem sapwood area, and (2) estimates of shoot silhouette area index (SSAI) based on measurements of shoot silhouette to total needle area ratios (STAR). An equation of the relationship between SSAI, leaf area index and the mean silhouette to total area ratio of shoots was derived.

Theory

Principle behind the LAI-2000 plant canopy analyzer

The LAI-2000 plant canopy analyzer (Li-Cor, Inc., Lincoln, NE) is designed to estimate leaf area index of plant canopies indirectly from measurements of radiation above and below the canopy, based on a theoretical relationship between leaf area and canopy transmittance. Its optical sensor comprises five detectors, arranged in concentric rings, that measure radiation (below 490 nm) from different sections of the sky. Canopy transmittance for these different sections is computed as the ratio between below-canopy and above-canopy readings for each detector ring. The leaf area estimate is based on the assumption of randomly distributed foliage elements. Other assumptions are that (1) foliage is optically black (all-absorbing) in the wavelength region below 490 nm, (2) foliage elements are small compared to the area of view of each ring, and (3) foliage is randomly oriented with respect to azimuth. The theoretical background is, briefly, as follows.

It may be shown that, in a horizontally homogeneous canopy with randomly distributed, infinitely thin, planar leaves, the mean transmittance (gap probability), T, is given by (e.g., Nilson 1971)

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

where (θ,ϕ) (θ = zenith angle, ϕ = azimuth) is the view direction (direction of projection), G is the ratio between projected and one-sided leaf area when projected in direction (θ,ϕ), and L is the one-sided leaf area index. The quantity GL then represents the projected leaf area index, defined as the total projected area of leaves (on a plane perpendicular to the direction of projection) per unit of canopy ground area.

From Equation 1, it follows that

$$G(\theta,\phi)L = -\ln[T(\theta,\phi)]\cos\theta. \tag{2}$$

Further, it can be shown (e.g., Miller 1967) that

$$\frac{1}{2\pi}\int_0^{2\pi}\int_0^{\pi/2} LG(\theta,\phi)\sin\theta\, d\theta\, d\phi = \frac{L}{2}, \tag{3}$$

i.e., that the spherically projected leaf area index (the left-hand side of Equation 3) is equal to one half of the one-sided leaf area index.

According to the assumptions, G is independent of azimuth and we may denote $G(\theta) = G(\theta,\phi)$. From Equations 2 and 3, it follows that

$$L = 2\int_0^{\pi/2} G(\theta)L\sin\theta\, d\theta = \int_0^{\pi/2} -2\ln[T(\theta)]\cos\theta\sin\theta\, d\theta. \tag{4}$$

Equation 4 implies that the leaf area index (L) can be estimated from the distribution of canopy transmittance over the upper hemisphere without information on the angular distribution of leaves, which generates the function G.

Computation method

The leaf area estimate provided by the LAI-2000 ($L^{\text{Li-Cor}}$) is obtained by approximating Equation 4 with the sum (see LAI-2000 plant canopy analyzer, instruction manual. Li-Cor, Inc., Lincoln, Nebraska, USA):

$$L^{\text{Li-Cor}} = -2\sum_{j=1}^{5}\left[\frac{1}{n}\sum_{i=1}^{n}\ln(\mathrm{tr}(i,j))\right]\cos\theta_j w_j , \tag{5}$$

where the spatial average ($i = 1,\ldots,n$) of the logarithms of transmittance ($\mathrm{tr}(i,j)$ = ratio of below-and above-canopy readings) for each ring (j) (θ_j = ring midpoint = 7°, 23°, 38°, 53° and 68°) is used as an estimate of $\ln[T(\theta)]$, and w_j (= 0.034, 0.104, 0.160, 0.218 and 0.494) are the weighing factors corresponding to $\sin\theta\, d\theta$.

The transmittances $\mathrm{tr}(i,j)$ in Equation 5 are averaged over the azimuth and represent mean values for the area seen by each detector. In computing $L^{\text{Li-Cor}}$, the average of logarithmic transmittances is used instead of the logarithm of average transmittances. The principle behind this method is that, if the canopy consists of homogeneous regions with different leaf area density, averaging the transmittance over these regions would give an underestimate of the leaf area index (Lang and Xiang 1986).

Application to coniferous stands: effect of needle shape and shoot structure

The theory described in Equations 1–4 was based on the assumption of infinitely thin, planar leaves that are randomly distributed in the canopy. However, Equations 1 and 2 apply generally in any canopy with randomly distributed foliage elements (e.g., leaves, needles or shoots) provided that G and L are defined so that GL represents the projected foliage area index, defined as the sum of projection areas of the individual foliage elements (on a plane perpendicular to the direction of projection) divided by the ground area covered by the canopy (Stenberg et al. 1994). The difference resulting from the choice of foliage element is reflected in the value of G, which depends on the geometrical shape of these elements.

To demonstrate the effect of needle shape and grouping into shoots on the LAI-2000 estimates, we considered two hypothetical cases: a canopy with randomly distributed needles (Case 1), and a canopy with randomly distributed shoots (Case 2).

Case 1. Canopy with randomly distributed needles

The principle behind Equation 3 is that when a body of convex shape is projected spherically, i.e., in all directions of a sphere (or hemisphere), the average projected area equals one fourth of its total surface area (e.g., for a sphere these are πr^2 and $4\pi r^2$) (Lang 1991). Thus, Equation 3 is valid for any convex foliage elements if G

and L are defined on a "half of total surface area basis" (Chen and Black 1992), and the spherically projected foliage area index is $L/2$. Consequently, $L^{\text{Li-Cor}}$ (Equation 5), represents one half of the total all-sided leaf area index.

In the case of infinitely thin, planar leaves, half the total leaf surface area is equal to one-sided leaf area, and $L^{\text{Li-Cor}}$ therefore represents the one-sided leaf area index. For coniferous needles, however, half the total surface area is more than the projected or one-sided needle area. If we denote the total all-sided needle surface area index by L_t, the projected needle area index by L_p and the ratio between these by c, the relation is:

$$L^{\text{Li-Cor}} = L_t/2 = c/2L_p. \tag{6}$$

In conclusion, in a canopy with randomly distributed needles, Equations 1 to 4 apply if G and L are defined on a total surface area basis ($L = L_t/2$), and $L^{\text{Li-Cor}}$ represents the needle area index taken as half of the total surface area.

Case 2. Canopy with randomly distributed shoots

Let L denote canopy leaf area index on a half of total surface area basis. Assuming shoots to be randomly distributed in the canopy, Equations 1 and 2 apply with GL defined as the projected shoot area index, i.e., G is now the ratio between projected shoot area (shoot silhouette area) and half the total needle surface area. However, Equation 3 is no longer valid, because the shoot is not a convex body (i.e., there is mutual shading between needles on a shoot). We define shading factor β (<1) so that (cf. Equation 3):

$$\frac{1}{2\pi}\int_0^{2\pi}\int_0^{\pi/2} LG(\theta,\phi)\sin\theta\,\mathrm{d}\theta\,\mathrm{d}\phi = \beta L/2. \tag{7}$$

The left-hand side of Equation 7 is the spherically projected shoot area index, and β represents the ratio of spherically projected shoot area to the spherically projected needle area (which is $L/2$). The value of $1 - \beta$ represents the mean fractional decrease in shoot projected area (silhouette area) resulting from shading among needles on a shoot.

Because the shoots are assumed to be randomly oriented with respect to azimuth we may write $G(\theta) = G(\theta,\phi)$. From Equation 7 then follows:

$$L = \frac{2}{\beta}\int_0^{\pi/2} LG(\theta)\sin\theta\,\mathrm{d}\theta = \int_0^{\pi/2}\frac{-2}{\beta}\ln[T(\theta)]\cos\theta\sin\theta\,\mathrm{d}\theta, \tag{8}$$

and the relation between $L^{\text{Li-Cor}}$ (computed based on Equation 5) and L is now found to be

$$L^{\text{Li-Cor}} = \beta L = 2\int_0^{\pi/2} LG(\theta)\sin\theta\,\mathrm{d}\theta, \tag{9}$$

The quantity βL is defined as the shoot silhouette area index, SSAI.

Materials and methods

Measurements with the LAI-2000 plant canopy analyzer were made in six experimental plots of Scots pine (*Pinus sylvestris* L.) at Jädraås Ecological Research Station in central Sweden (60°49′ N, 16°30′ E). The plots were part of an irrigation and fertilization experiment that was initiated in 1974 (cf. Aronsson et al. 1977). The treatments consisted of control (C), irrigation (I), solid fertilization (F) and irrigation combined with a complete liquid fertilizer (IL). The plot size was 30 × 30 m and there were initially five replicates, but one plot of each treatment was harvested in 1981. Further information about treatments and experimental results have been summarized by Linder (1987, 1990).

For the measurements with the LAI-2000, duplicate plots of C, I and F were chosen (Table 1). The plots were measured on two occasions, August 21–23 and October 15–16, 1990. Below-canopy measurements were made at 100 points, marked by stakes located systematically at 1-m intervals, in the central 100 m^2 (10 × 10 m) region of each plot. Above-canopy measurements were taken automatically every 15 s by a second instrument in the center of an open field situated nearby. A view restrictor of 90° was used in all measurements to prevent direct sunlight from reaching the sensor and at the same time to occlude the measuring person from the area of view. In taking canopy measurements the sensor was held so that the same portion of the sky was occluded for both sensors (above- and below-canopy measurements).

The weather conditions during measurements included both sunny and cloudy skies. On three plots, duplicate LAI-2000 estimates were obtained separately for sunny and cloudy conditions (mean values shown in Table 1). On the control plots (C15 and C18), the weather was sunny, and on plot I06 the weather was cloudy during both measurements (August and October). On plot I17, the August measurement was made under cloudy skies, and in October LAI-2000 estimates were

Table 1. Stand characteristics and estimates of leaf area index.[1]

Plot	No. of trees (ha^{-1})	BA m^2 ha^{-1}	L	$L^{\text{Li-Cor}}$	ΔL (%)	$\Delta L^{\text{Li-Cor}}$ (%)
C15	1375	14.6	2.66	1.56	–17	+1
C18	1300	11.1	1.98	1.08	–17	–6
I06	1325	15.0	2.74	1.61	–22	–6
I17	1375	15.8	2.84	1.62	–17	–5
F05	1175	23.5	4.35	2.71	–18	–3
F19	1425	28.9	5.41	2.79	–15	–2

[1] Abbreviations: C = control plot, I = irrigated plot, F = fertilized plot. Plot numbers as in Aronsson et al. (1977). BA = Basal area (under bark) at breast height (1.3 m). L = Estimate of leaf area index based on sapwood area, $L = L_t/2$. $L^{\text{Li-Cor}}$ = Estimate of leaf area index by LAI-2000 (mean value for duplicates). ΔL, $\Delta L^{\text{Li-Cor}}$ = Change in leaf area index from August to October 1990.

obtained for both sunny and cloudy conditions. On plot F05, the August measurement was made under sunny skies, and in October estimates were obtained for both sunny and cloudy conditions. On plot F19, measurements in August were made in both sunny and cloudy conditions, and the October measurement was made in sunny conditions. For the three duplicate LAI-2000 measurements, estimates obtained in sunny conditions were 0.4% (F05), 4% (I17) and 8% (F19) smaller than the corresponding estimates obtained in cloudy conditions.

The independent estimate of leaf area index in August 1990 was calculated based on the empirically derived regression between projected (flat side) needle area index (L_p) and cross-sectional sapwood area (SA, m^2 ha^{-1}) (cf. Waring and Schlesinger 1985). The value of $L_p = 0.18SA$ was determined in the stand and covered the range of treatments. The estimate of cross-sectional sapwood area was based on measurements of the diameter at breast height of all trees within the measurement plots. The amount of heartwood in each of five size classes of trees was determined by coring. The leaf area index on a half of total surface area basis (L) was obtained by multiplying L_p by 1.35, i.e., assuming the ratio $c = 2.7$ (Equation 6) of total to projected needle area (Flower-Ellis and Olsson 1993). The difference in L between August and October was estimated from measurements of needle length in litter traps, based on the regression of needle area on single needle length (Flower-Ellis and Olsson 1993). Stand characteristics and estimates of leaf area index are presented in Table 1.

Calculations

The relation between β (Equation 7) and the silhouette to total area ratio (STAR) of shoots was derived as follows. Let $SA_s(\theta, \phi)$ denote the silhouette area (projection area not including gaps between needles) of a shoot, when projected on a plane perpendicular to the direction (θ, ϕ) (θ = zenith angle, ϕ = azimuth), and let A_n denote the total all-sided needle surface area of the shoot. The mean silhouette to total area ratio ($\overline{\text{STAR}}$) with respect to a spherical shoot orientation, i.e., the mean STAR of a shoot projected in all directions of the sphere, is defined as (Oker-Blom and Smolander 1988):

$$\overline{\text{STAR}} = \frac{1}{2\pi}\int_0^{2\pi}\int_0^{\pi/2}\frac{SA_s(\theta,\phi)}{A_n}\sin\theta d\theta d\phi. \tag{10}$$

Note that $\overline{\text{STAR}}$ in Equation 10 is defined for a single shoot. It depends on shoot structure but (being a spherical average) does not depend on the direction of the shoot in the canopy. Let $f(k)$ denote the fraction of leaf area of shoots in the canopy having a mean silhouette to total area ratio equal to $\overline{\text{STAR}}(k)$. The ratio between spherically projected shoot area and total needle surface area of all shoots in the canopy is then

$$\overline{\text{STAR}}_{\text{canopy}} = \sum_k \text{f}(k)\overline{\text{STAR}}(k). \tag{11}$$

Because the shading factor β is the ratio between spherically projected shoot area and spherically projected needle surface area (which is one fourth of the total needle surface area), we obtain

$$\beta = 4\,\overline{\mathrm{STAR}}_{\mathrm{canopy}}, \tag{12}$$

i.e., β is four times the (needle area weighted) $\overline{\mathrm{STAR}}$ of the canopy.

To estimate the shading factor β (Equation 7), the silhouette areas of 133 shoots were measured by the technique described by Oker-Blom and Smolander (1988). The shoots were sampled from leader shoots and first-order lateral shoots on the fourth whorl of three mean trees from each of the three treatments (C, I, and F) and represented three age-classes of foliage; current-year, one- and two-year-old (for details see Smolander et al. 1993). The $\overline{\mathrm{STAR}}$ in different age classes for the Jädraås data is shown in Figure 1. In addition to these data, measurements of $\overline{\mathrm{STAR}}$ of 429 other Scots pine shoots were available for the estimation of β (Oker-Blom and Smolander 1988, Smolander et al. 1993).

In none of the studies was the sampling procedure designed to give an estimate of the canopy mean STAR ($\overline{\mathrm{STAR}}_{\mathrm{canopy}}$); however, as the combined data set includes a large variation in site fertility, shoot age and position in the crown, it gives information on the variation in $\overline{\mathrm{STAR}}$ and an estimate of the consequent range of β.

Results and data analysis

Comparison of estimates of leaf area index

Estimates of leaf area index by the LAI-2000 ($L^{\mathrm{Li\text{-}Cor}}$) in August 1990 were on average 43% smaller then the estimate (L) based on the regression on sapwood area

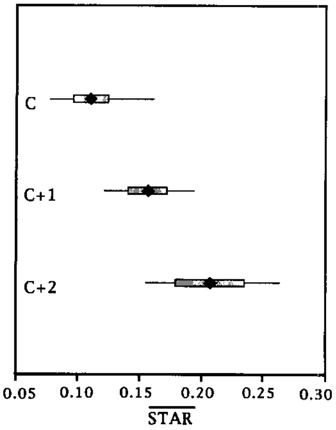

Figure 1. The mean STAR of current-year (C), one-year-old (C + 1) and two-year-old (C + 2) shoots of the 133 sample shoots taken at Jädraås research site, with bars showing the variation (thin line) and standard deviation (thick line).

(Figure 2). Consequently, when L was multiplied by the factor $\beta = 0.57$ to represent the shoot silhouette area index (SSAI), a good agreement was found (Figure 3). The value of 0.57 for β corresponds to $\overline{\mathrm{STAR}}_{\mathrm{canopy}} = 0.142$ (Equation 12), which happens to be equal to the $\overline{\mathrm{STAR}}$ of Oker-Blom and Smolander (1988).

The decrease in leaf area index as a result of litterfall between the two measurement dates was only partly detected by the LAI-2000. Although the decrease in L from litterfall occurring between late August and mid-October varied between 15 and 22%, differences in $L^{\text{Li-Cor}}$ were less than 6% (Table 1). As a result, SSAI estimated as the August value reduced by ΔL (i.e., assuming β to have remained unchanged at 0.57) was smaller than $L^{\text{Li-Cor}}$ (Figure 4).

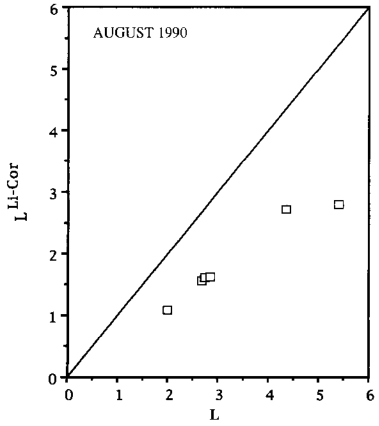

Figure 2. Estimates of leaf area index from the regression on sapwood area (L) and by the LAI-2000 ($L^{\text{Li-Cor}}$) for the six plots measured in August 1990, with the 1/1 line shown for comparison.

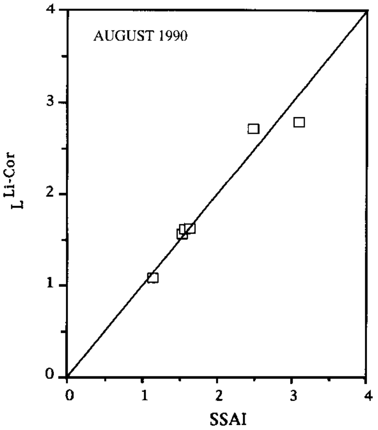

Figure 3. Comparison of $L^{\text{Li-Cor}}$ measured in August 1990 and the shoot silhouette area index (SSAI) calculated as SSAI = $0.57L$ (to give best fit to the 1/1 line).

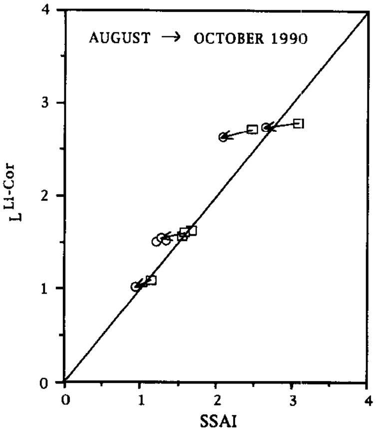

Figure 4. Comparison of $L^{\text{Li-Cor}}$ and SSAI (estimated as 0.57L) in August (□) and October (○).

Data from the August measurement were used for a more careful analysis of the method and results

Estimates based on a reduced area of view

Plot areas were not large enough to cover completely the area of view of the sensor, i.e., at the largest zenith angles the detector (Ring 5) would see part of the neighboring plots. Therefore, we studied the effect of neglecting Ring 5 in calculating $L^{\text{Li-Cor}}$. The estimate of LAI-2000 based on detector Rings 1–4 was calculated by (Jon Welles, personal communication):

$$L^{\text{Li-Cor(4)}} = -2\sum_{j=1}^{4}\left[\frac{1}{n}\sum_{i=1}^{n}\ln(\mathrm{tr}(i,j))\right]\cos\theta_j w'_j\,, \tag{13}$$

where $w'j$ (= 0.034, 0.103, 0.158, and 0.705) are the new weighting factors for Rings 1–4.

Because the weights (w_j and $w'j$) (Equations 5 and 13) always total unity, the effect of neglecting one or more rings in calculating $L^{\text{Li-Cor}}$ depends on the values of the contact number (K) for different rings, defined as:

$$K(\theta_j) = \left[\frac{1}{n}\sum_{i=1}^{n}\ln(\mathrm{tr}(i,j))\right]\cos\theta_j\,. \tag{14}$$

By theory, K is independent of view direction only if the angular distribution of foliage is spherical.

Estimates of leaf area index calculated based on Rings 1–4 ($L^{\text{Li-Cor(4)}}$) changed by less than 5% on three of the plots (C15, C18 and I06), but increased by 9–13% on the other plots, indicating that the contact number was smaller for Ring 5. Possible reasons for this, which would justify neglecting Ring 5 (aside from side plot contamination), might be increased scattering at large zenith angles or because our above-canopy readings at angles near the horizon may have had some side shading. The scattering error can be huge in sunny conditions, when leaf area index is low and much of the foliage seen by the sensor is sunlit (Jon Welles, personal communication). However, in this study the biggest differences caused by neglecting Ring 5 occurred in the most dense stands (I17, F05 and F19), and were of the same magnitude in sunny and cloudy conditions.

The difference in estimates may also be a result of a non-spherical shoot orientation, in which case it would not be justified to estimate L based on Equations 3 and 4 using a reduced number of rings (Equation 13). The principle behind Equation 3 is that, by averaging over the upper hemisphere, the effect of foliage angle distribution is eliminated. If the area of view is reduced, the theory no longer applies (unless the foliage angle distribution is spherical), and calculations based on a reduced number of rings would give biased estimates. The potential error depends on how much the actual foliage angle distribution deviates from a spherical distribution.

An alternative approach for computing L (included as an option in the LAI-2000 software program) is to use the method developed by Lang (1987), which is based on approximating the contact number $K(\theta)$ as a linear function of the zenith angle (θ). This method can be used to compute L based on any pair or subset of zenith angles; however, the accuracy decreases as the number of angles used decreases. In the study by Chason et al. (1991), conducted in an oak-hickory forest, estimates increased continuously as higher zenith angles were sequentially omitted. The computed estimate based on Rings 1 and 2 alone agreed best with an independent estimate from litterfall collections, however, the improvement from neglecting rings obviously occurred for the wrong reason.

Estimates based on averaging the transmittance

Table 2 gives the mean and standard deviation of canopy transmittance to diffuse (isotropic) radiation ($\mathrm{tr_d}$) at the 100 measurement points of each plot, derived from

Table 2. Canopy transmittance and extinction coefficients for diffuse (isotropic) radiation.

Plot	$\mathrm{tr_d}$[1]	L_t[2]	k_d[3]
C15	0.317 (0.047)	5.32	0.216
C18	0.457 (0.058)	3.97	0.197
I06	0.303 (0.069)	5.48	0.218
I17	0.294 (0.063)	5.67	0.216
F05	0.117 (0.018)	8.69	0.247
F19	0.101 (0.017)	10.8	0.212

[1] $\mathrm{tr_d}$ = Mean canopy transmittance to diffuse isotropic radiation, with values of the standard deviation (over measurement points) in parenthesis.

[2] L_t = All-sided leaf area index.

[3] $k_d = -\ln(\mathrm{tr_d})/L_t$ = Canopy extinction coefficient for isotropic radiation.

the LAI-2000 data. At each point of measurement (i), the canopy transmittance to isotropic radiation was approximated by the sum

$$\mathrm{tr_d}(i) = 2\sum_{j}\mathrm{tr}(i,j)w''_{\mathrm{j}}\,, \tag{15}$$

where $\mathrm{tr}(i,j)$ is the transmission of section j and $w'j$ (= 0.066, 0.189, 0.247 and 0.249) are the weights ($\sin\theta\cos\theta d\theta$) attributed to the different sections. Table 2 also shows the extinction coefficients (k_d) to isotropic radiation, defined as $k_\mathrm{d} = -\ln(\mathrm{tr_d})/L_\mathrm{t}$.

The variation in the sectional transmittance $\mathrm{tr}(i,j)$ at different points (i) is of interest when evaluating the computation method (Equation 5) of the LAI-2000. If there was no variation in transmittance, it would make no difference in which order the mean is computed or the logarithm of the transmittance of each ring is taken. When there is variation, however, the method used (averaging logarithms) leads to a higher leaf area estimate than would be obtained by using the logarithm of the average transmittance of each section (ring).

Theoretically, it can be shown that the spatial average transmittance over an infinite horizontal region beneath a homogeneous canopy converges to T, as defined by Equation 1. At any one point, however, the transmittance in a fixed direction is either 0 or 1, and the smaller the region over which the averaging is done, the larger the stochastic variation around the expected value (T). Thus, to obtain an accurate estimate of the leaf area index, a spatial average of transmittances over a large enough area must be used.

If the canopy was homogeneous, with no variation in leaf area density, the best estimate would be obtained by averaging transmittance over the whole area before taking the logarithm. In contrast, if the canopy consisted of homogeneous regions each with a different leaf area density, averaging the logarithms of transmittance over these different regions would give the best estimate of the average leaf area index (Lang and Xiang 1986).

The latter method seems to be justified in a forest canopy where there is considerable variation in foliage density, e.g., within and between crowns. However, to obtain the correct estimate by averaging the logarithms of sectional transmittances (Equation 5), each transmittance value should represent an area that is homogeneous and large enough to give a stable mean value. In applying Equation 5 to calculate $L^{\text{Li-Cor}}$, it is implicitly assumed that the spatial variation in sectional transmittance reflects real differences in leaf area density of the canopy seen by the detector at different points, and not natural stochastic variation around an expected value. If this is not true, the method will theoretically overestimate the leaf area index.

The spatial variation in canopy transmittance for the different sections of the sky decreases with increasing zenith angle (Figure 5), because the regions represented (measured) by the detector rings become larger with increasing zenith angle. In addition, the canopy becomes apparently more homogeneous at near-horizontal view angles. Leaf area estimates based on taking the logarithm of the spatial mean transmittance at each zenith angle (ring) were 15–20% smaller than those given by

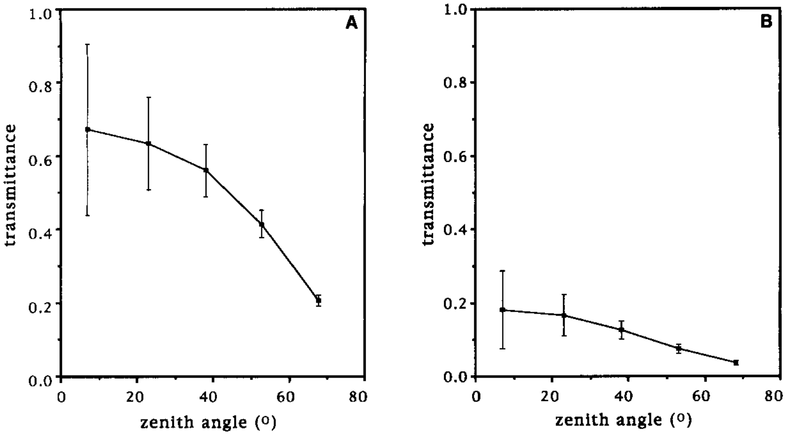

Figure 5. Mean and standard deviation of the sectional transmittances at plots C18 (A) and F19 (B), measured by the LAI-2000 in August 1990.

the LAI-2000, which takes the mean of the logarithms (Equation 5). This difference results mainly from the large variation in transmittance at near-zenith angles (Figure 5). At these angles, much of the variation can be assumed to reflect real differences in leaf area density within and between crowns, which would justify the method used.

Conclusions

This study supports the hypothesis that in coniferous forests the LAI-2000 plant canopy analyzer gives an estimate of shoot silhouette area index rather than leaf area index. The theory behind the LAI-2000 is based on the assumption of randomly distributed foliage elements, i.e., leaves, needles or shoots. It was shown that, in a canopy of randomly distributed leaves or needles (Case 1), the estimate obtained by the LAI-2000 ($L^{\text{Li-Cor}}$) represents the leaf area index on a half of total surface area basis ($L = L_t/2$, where L_t is all-sided leaf area index). For flat leaves, half of the total surface area is equal to the one-sided leaf area, but for non-flat leaves such as pine needles, L is larger than the leaf area index based on a projected or one-sided area.

Under the assumption of randomly distributed shoots (Case 2), it was shown theoretically that the LAI-2000 estimate ($L^{\text{Li-Cor}}$) represents a shoot silhouette area index (SSAI) defined as SSAI = βL, where the factor β is equal to the ratio of spherically projected shoot area to spherically projected needle area. When L was multiplied by $\beta = 0.57$, which would correspond to a canopy $\overline{\text{STAR}}$ value of 0.142, good agreement was found between the resulting estimate of SSAI and $L^{\text{Li-Cor}}$. A canopy $\overline{\text{STAR}}$ = 0.142 seems reasonable for Scots pine (Oker-Blom and Smolander 1988, Smolander et al. 1993); however, it must be recognized that this value was not obtained as an independent estimate but as the value giving the best fit between $L^{\text{Li-Cor}}$ and SSAI (Figure 3). Nonetheless, the result suggests that in Scots pine, as opposed to Douglas-fir (cf. Smith et al. 1993), estimates by the LAI-2000 can be corrected by simply accounting for the grouping of needles into shoots.

The decrease in leaf area index due to litterfall occurring between August and October 1990 was only partly detected by LAI-2000. Changes in weather conditions between the two measurements (e.g. from sunny in August to cloudy in October) could theoretically produce such an effect, but this was not the case in this study. The result therefore indicates that the shoot silhouette area did not change to the same degree as the needle area, i.e., that there was an increase in β between the two measurement dates. The large increase in STAR with age found for Scots pine in this study (Figure 1) and by Smolander et al. (1993) suggests that β varies seasonally. The variation in STAR with age and possible effects of other factors, such as shoot order and position in the crown implies, however, that more research is needed to obtain reliable estimates of the mean canopy STAR and its seasonal variation.

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