

Assessing seasonal leaf area dynamics and vertical leaf area distribution in eastern white pine (*Pinus strobus* L.) with a portable light meter

JAMES M. VOSE and WAYNE T. SWANK

USDA Forest Service, Southeastern Forest Experiment Station, Coweeta Hydrologic Laboratory, NC 28763, USA

Summary

We evaluated the ability of a portable light meter (Sunfleck Ceptometer, Decagon Devices, Pull USA) to quantify seasonal photosynthetically active radiation (PAR, 400–700 nm) intercepted stand leaf area index (LAI), and vertical LAI distribution in a 32-year-old eastern white pine (*Pinus strobus* L.) plantation. Canopy PAR transmittance measured with the ceptometer was converted with the Beer-Lambert Equation. The ceptometer was sensitive to changes in PAR transmittance resulting from foliage growth. Predicted stand LAI ranged from 3.5 in the dormant season to a maximum of 5.3 in late July. Predicted LAI values were within 9% of values determined from destructive sampling. Published canopy extinction coefficients (k) were inadequate for converting PAR transmittance to stand LAI because a significant amount of PAR was intercepted by dead branches and stems in the forest canopy. Because of interception by dead branches and stems, we estimated $k = 0.84$, substantially higher than previously reported values. The ceptometer was also sensitive to changes in PAR transmittance within the canopy. However, in contrast to predictions based on Beer-Lambert Law, the relationship between proportional PAR transmittance (Q_i/Q_o) and vertical LAI within the canopy was linear. Thus, vertical LAI distribution was best estimated with a linear relationship as opposed to the non-linear model assumed in the Beer-Lambert Equation. We hypothesize that the linear relationship was a result of a gap in the canopy which was not represented by the cumulative area distribution estimation procedure.

Introduction

Knowledge of the quantity and vertical distribution of leaf area index (LAI) in a forest stand is important for understanding forest structure and productivity (e.g., Grier and 1982, Gholz 1982, Vose and Allen 1988, Vose 1988), water use (Grier and 1977, Swank et al. 1988), and atmospheric deposition to the forest canopy (Lindberg 1982). In many pine species, LAI varies considerably (e.g., Kinerson et al. 1974) over the growing season because of short needle retention times. For example, Kinerson et al. (1974) found that the pattern of seasonal LAI development in loblolly pine (*Pinus taeda* L.) was unimodal, with development of new foliage beginning in early spring, peak LAI occurring in late summer, and senescence of old foliage reducing LAI in the autumn; LAI varied by approximately 50% over the year. Quantifying foliar dynamics in a stand is difficult using traditional approaches such as destructive sampling, sapwood-leaf area relationships, or allometric regression because they are labor intensive, difficult to conduct on a repeated basis, or insensitive to small changes in LAI. Needle and branch elongation have been measured at repeated intervals during the growing season (Harms 1971, Kinerson et al. 1974).

this approach is labor intensive and requires access to branches in mature stands.

The objective of this study was to evaluate the Sunfleck Ceptometer (Decag Devices, Pullman, WA, USA) for quantifying seasonal radiation interception, projected stand LAI, and projected vertical LAI distribution in eastern white pine (*Pinus strobus* L.). White pine LAI varies considerably during the year. In each growing season it produces a new cohort of foliage which is generally retained only until the autumn of the following year. Thus, in its southern range, white pine has a single age class of foliage through the dormant season and two age classes (previous year's developing foliage) in the growing season. Pierce and Running (1988) evaluated the ceptometer for predicting stand LAI in lodgepole pine (*Pinus contorta* Dougl.), but they did not examine its utility for quantifying seasonal LAI dynamics or vertical LAI distribution.

Materials and methods

Site and stand description

The study was conducted in a 32-year-old white pine plantation (Watershed 1) at the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains of western North Carolina, USA. Watershed 1 (WS 1) is 16.1 ha, has, overall, a southerly aspect and spans an elevation range of 715 m to 990 m. Soils are mesic Typic Hapludults of the Fannin soil series. Mean annual rainfall at a nearby climatic station (675 m) is 1790 mm. During the first eight months of 1989, which encompassed the period of the study, precipitation was 316 mm above average. Mean annual temperature is 12.6 °C and ranges from an average of 6.7 °C in the dormant season to 18.5 °C in the growing season.

Leaf area index was estimated on five, 0.08-ha rectangular plots within WS 1 (Table 1). Four plots are part of a larger network of 20 permanent plots on which tree diameter at breast height (DBH) and tree density (stems ha⁻¹) have been measured at intervals of about 5 years since 1967. The most recent measurement was conducted in 1985. The fifth plot was associated with another study and was measured for DBH and tree density in 1989. Projected LAI's in Table 1 are dormant season estimates.

Table 1. Stand and site characteristics of plots used to estimate stand leaf area index (LAI in m² m⁻²)

Plot	Basal area (m ² ha ⁻¹)	Stems ha ⁻¹	Elevation (m)	Slope (%)	Aspect	LAI
1	40.3	790	717	40	S30E	3.0
2	51.6	1556	732	46	S2W	2.9
3	48.2	1013	854	36	S4E	2.9
4	54.4	1939	823	42	W	3.8
5	56.2	1260	777	50	S89W	3.2
\bar{X} =	50.1	1154	—	43	—	3.2

Ceptometer description

A thorough description of the ceptometer and its theory of operation for estimating LAI are given in Pierce and Running (1988). Briefly, the ceptometer measures photosynthetically active radiation (PAR, 400–700 nm) incident on 80 sensors located at 1 cm intervals along a narrow, 80 cm probe. The ceptometer automatically calculates and displays the arithmetic average of the 80 sensor measurements.

Canopy PAR transmittance and total incoming PAR in open areas were used to compute LAI using the Beer-Lambert Equation:

$$\text{LAI} = -\ln(Q_i / Q_o) / k,$$

where Q_i = canopy PAR transmittance, Q_o = total incoming PAR, and k = light extinction coefficient (the k used for determining LAI in our study is given in a following section). This calculation assumes that foliage is randomly distributed in the canopy, and that leaf inclination angles are spherically distributed in the canopy. However, as discussed in Jarvis and Leverenz (1983) and Pierce and Running (1988), the Beer-Lambert Equation is fairly insensitive to violations of these assumptions.

Below canopy PAR transmittance sampling

Canopy PAR transmittance was measured from ten randomly located and permanently marked locations within each of the five measurement plots. At each location, ten measurements of canopy transmittance were taken, averaged, and stored. To obtain the ten measurements, the ceptometer was rotated 360° above each location and PAR transmittance readings were taken at approximately 36° intervals. Canopy transmittance for each plot and sample period was represented by the average of ten measurements (arithmetic mean of 80 sensors × ten samples per location). Samples were obtained on clear days usually between 1100 and 1400 h solar time. Total incoming PAR was measured in large, open areas at the beginning, midpoint, and end of the sampling period. Total incoming PAR values measured during the time period closest to the individual plot measurement time period were used in the Beer-Lambert Equation.

Measurements were made six times during 1989. Sampling began before initiation of new foliage growth in late April (Julian day 117) and ended after cessation of foliage growth in late August (Julian day 242). The interval between sampling periods was between 20 and 36 days, with a mean of 25 days. Maximum sun angle which occurred at the midpoint of each sample period (i.e., 1230 h), ranged from 17° (Julian day 117) to 78° (Julian day 189) (Smithsonian Meteorological Tables). Sun angle variation over the 1100 to 1400 h sampling period was less than 10°.

Within-canopy PAR transmittance sampling

The distribution and seasonal change in LAI within the canopy were measured using a 30 m “walk-up” tower located at the base of Plot 1. Canopy PAR transmittance was measured at 2 m vertical intervals beginning at 1.4 m above ground and ending at 29.6 m.

above the canopy. At each interval, 12 measurements were taken (six at two corners of the tower) by extending the ceptometer at arm's length and rotating 180°. Measurements were taken at approximately 30° intervals. Thus, at each interval canopy PAR transmittance was represented by 12 measurements (arithmetic mean of 80 sensors \times 12 samples). Measurements were obtained on clear days between 1230 and 1300 h solar time.

Vertical PAR transmittance was measured five times in 1989. Sampling began in mid-May (Julian day 137) and ended in late August (Julian day 242). The interval between sample periods was 20 to 30 days, with a mean of 26 days. At each measurement period, a random sample of foliage was examined to determine the length of new needles relative to the length of needles produced the previous year.

Canopy light extinction coefficient determination

The extinction coefficient used to convert PAR to stand LAI was obtained by solving the Beer-Lambert Equation for k using canopy PAR transmittance values (before k expansion) from 20 random locations within WS 1 (i.e., 20 locations \times 10 measurements \times arithmetic mean of 80 sensors = 200 measurements) and a dormant stand LAI value of 3.1. This LAI value was based on a destructive sample of trees in 1985 which was extrapolated to the stand using a mean tree approach (Swank and Schreuder 1973). Because k depends on sun angle (Sinclair and Knoerr 1980), canopy PAR transmittance measurements used for estimating k were taken over the same time interval used for stand LAI determinations (i.e., 1100 and 1400 h solar time). Adopting this approach, we calculated a k of 0.84 and used it to convert PAR to LAI for all sample periods and plots. We also evaluated the use of published values for determining stand LAI from ceptometer PAR measurements.

Destructive sampling determination of LAI and vertical LAI distribution

A separate estimate of LAI for our study plots (Table 1) was obtained using sampling procedures established in previous studies of biomass and surface area of the white pine plantations at Coweeta (Schreuder and Swank 1973, Swank and Schreuder 1974). Data were collected in 1985 from 16 trees which represented the range of tree diameters on Coweeta WS 1 and 17. Plot LAI was estimated by extrapolating sample tree surface area to the population using a ratio-of-means estimation procedure (Swank and Schreuder 1974). Determination of vertical LAI distribution entailed four computational steps which utilized measurements of node height above ground level, live crown length, and LAI by node (Schreuder and Swank 1974).

Results from repeated measurements of foliar surface area (Swank and Schreuder 1973, Vose and Swank, in press) indicate that there has been little year to year variation in canopy biomass since canopy closure at age 12. In addition, 1985 needle-fall biomass (4030 kg ha⁻¹) was within 7% of 1989 needle-fall biomass (4300 kg ha⁻¹). This difference is within the error term (11%) of the needle-fall biomass measurements. Results from repeated measurements and the correspondence between needle-fall biomass indicate that the 1985 LAI estimate is a reasonable estimate of LAI in 1989.

Results and discussion

Stand LAI and PAR transmittance

Ceptometer readings were sensitive to changes in canopy PAR transmittance from foliage production. Q_i/Q_o decreased from 0.0516 in late April before began to grow, to 0.0154 in late August when foliage growth was complete (1). In terms of LAI, this change represents an increase from 3.5 in late April in late August (Figure 1). Ceptometer LAI estimates before leaf expansion greater than destructive sample estimates (i.e., 3.5 for ceptometer *versus* destructive) for the same study plots (Table 1). This small difference is we measurement error of most LAI techniques. For example, Marshall and (1986) compared four LAI estimation techniques and found that LAI estimates the same stand ranged from 6.6 to 16.2. Possible reasons for the discrepancy LAI estimates in our study are inaccuracy in determining k , variability in Q_i/Q_o , and the inherent variability associated with estimating LAI from sampling. The peak LAI estimate of 5.3 agrees within 2% of peak LAI ϵ from previous studies on WS 1, where peak LAI since canopy closure (age remained at approximately 5.4 (Swank and Schreuder 1973, Vose and S press).

The $k = 0.84$ used to calculate LAI from Q_i/Q_o is substantially larger than previously reported values. Previous k values, also calculated at maximum stand density, have ranged from 0.28 to 0.62 for coniferous forests (Jarvis and Leverenz 1983, Sinclair and Knoerr 1982, Pierce and Running 1988). Using an average k of 0.50 for the genus *Pinus* (calculated from data in Jarvis and Leverenz 1983), Q_i/Q_o estimates, LAI ranges from 5.2 before foliar growth to a peak LAI of 5.3 in late July.

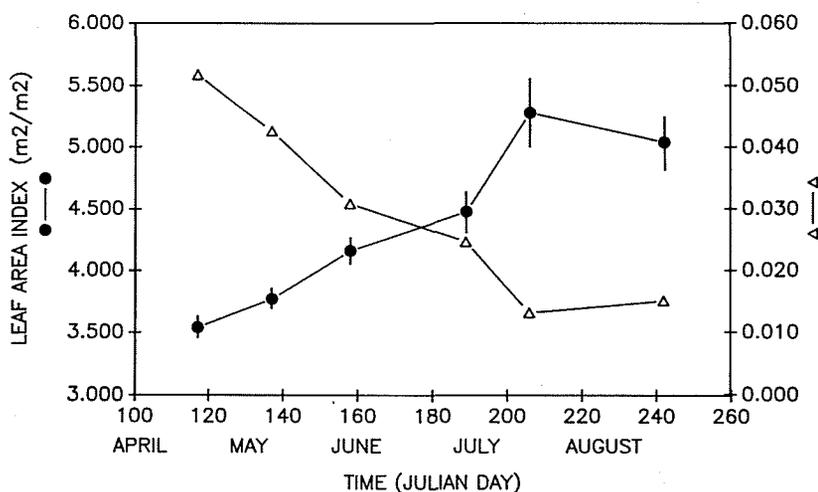


Figure 1. Seasonal leaf area index (LAI in $m^2 m^{-2}$) and the ratio of canopy PAR transmittance incoming photosynthetically active radiation (Q_i/Q_o). Standard error bars ($n = 5$) provided for

Based on destructive sampling, these LAI values are substantial overestimates. Extinction coefficients are typically calculated at the bottom of the forest canopy. However, our white pine stand contained a substantial quantity of dead branches, well as stem area, below the live canopy (Figure 2) that intercepted PAR. To illustrate this point, we used data from the final sample period, where Q_i/Q_o was 0.0732 at the bottom of the forest canopy (18 m) versus 0.0164 at ground level (Figure 1). Although not intended as a quantification of stem and branch area below the canopy, this equates to a difference in LAI of 3.0 (i.e., 5.2 at canopy bottom versus 8.2 at ground level) if $k = 0.50$ is used in the Beer-Lambert Equation. Thus, k values calculated at the bottom of the live crown do not account for PAR intercepted by dead branches and stems and will overestimate LAI if PAR values are obtained at ground level. In contrast to our study, Pierce and Running (1988) and Marshall and Waring (1986) found that published k values provided reasonable estimates of LAI for lodgepole pine and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), respectively. Although not mentioned or quantified in these studies, it appears that PAR interception by dead branches and stems was not a significant factor.

Within canopy PAR transmittance and LAI distribution

Seasonal changes in PAR transmittance within the canopy were detectable with a LiCor Li-190 quantum sensor (Figure 3). As sampling progressed from mid-May to late August, the percentage of developing needles were 7, 43, 57, 85 and 100% expanded relative to the past year.



Figure 2. Example of dead branch retention below the live canopy. Photograph was taken 4 m below the bottom of the live canopy.

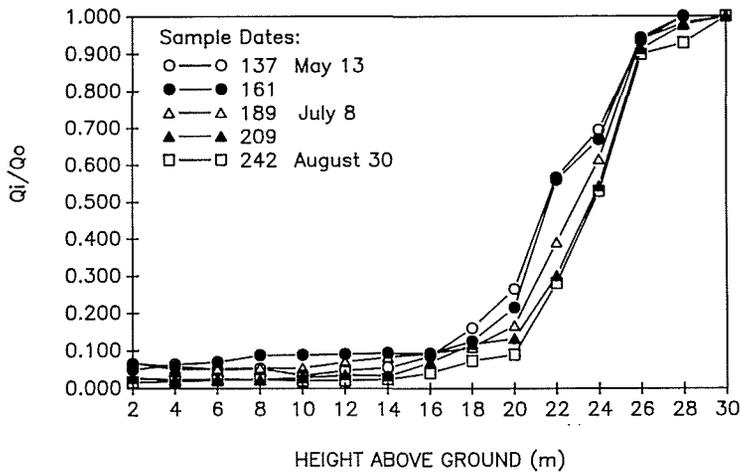


Figure 3. Seasonal Q_i/Q_o within the canopy. Measurements were obtained at 2 m intervals below ground level (2 m) and ending above the canopy.

needles, respectively. This phenological development is reflected in Figure 3, which shows that progressively less PAR was transmitted by the canopy as the canopy expanded and LAI increased.

We used Q_i/Q_o measurements and vertical LAI distribution data from destructive sampling to: (1) calculate a canopy extinction coefficient, (2) predict vertical distribution from Q_i/Q_o data, and (3) evaluate the appropriateness of the Beer-Lambert Equation for determining vertical LAI distribution. First, we quantified the vertical distribution of LAI within the canopy by distributing a plot LAI calculated with the ceptometer at ground level on Julian day 137, vertical LAI within the canopy using the percent distribution data in Table 2. Julian day 137 was chosen because new foliage was only slightly expanded (7%). Hence, canopy architecture was most similar to the dormant season LAI pattern determined from destructive sampling. Then, we regressed cumulative LAI against Q_i/Q_o to estimate

Table 2. Cumulative leaf area index (LAI in $\text{m}^2 \text{m}^{-2}$) distribution by canopy depth determined from destructive sampling in the dormant season.

Canopy depth (m)	Cumulative LAI ¹	% Distri
0–2	0.31	0.12
2–4	0.90	0.35
4–6	1.70	0.65
6–8	2.40	0.92
8–10	2.60	1.00

¹ Cumulative LAI was determined from a destructive sample of 16 trees in winter 1985. These data were used to determine the % distribution data shown above. The % distribution data were the same as those with LAI = 3.64 determined with the ceptometer on Julian day 137. Results are shown in

extinction coefficient. We found that a linear regression provided the best fit to the data ($r^2 = 0.98$) compared to the assumed exponential relationship between Q_i/Q_o and cumulative LAI within the canopy ($r^2 = 0.88$) (Figure 4). The linear relationship appears to be influenced by a gap in the canopy between 24 m and 22 m above ground (Figure 3) which resulted in only a 15% decrease in Q_i/Q_o (i.e., from $Q_i/Q_o = 0.66$ at 24 m to $Q_i/Q_o = 0.56$ at 22 m), while cumulative LAI predicted from the percent distribution data increased by a full unit over this interval. This gap appeared to “fill in” with foliage as needles grew and branches elongated, because in the final sampling period, Q_i/Q_o decreased by 46% from 24 m to 22 m (Figure 3). The slope of the linear regression (-0.41) using $\ln(Q_i/Q_o)$ data, which is equivalent to k , was within the range of k values reported for *Pinus*. We also predicted k using Q_i/Q_o data at the bottom of the live canopy and LAI = 3.64 (i.e., $k = -\ln(Q_i/Q_o)/\text{LAI}$). Interestingly, $k = 0.50$, which is equivalent to the average k value reported for the genus *Pinus*. In contrast to our results, Sinclair and Knoerr (1982) found a log-linear relationship between Q_i/Q_o and cumulative LAI for a loblolly pine canopy, as did Hagihara and Hozumi (1986) for cypress (*Chamaecyparis obtusa* (Sieb. and Zucc.) Endl.).

For comparison, we predicted vertical LAI distribution with the linear model, and the Beer-Lambert Equation using $k = 0.41$ and $k = 0.50$. As expected, the linear model provided a better characterization of vertical LAI distribution than the Beer-Lambert Equation (Figure 5). However, our results are limited because the within canopy Q_i/Q_o measurements were taken at only one location within the stand. In addition, because of the need for repeated measurements from the canopy, we could not quantify vertical LAI at our sample location with destructive sampling. Thus, our results depend on how well the percent distribution data obtained from destructive sampling reflected the vertical LAI distribution at our sample location. As noted previously, we hypothesize that the linear relationship we found was primarily the

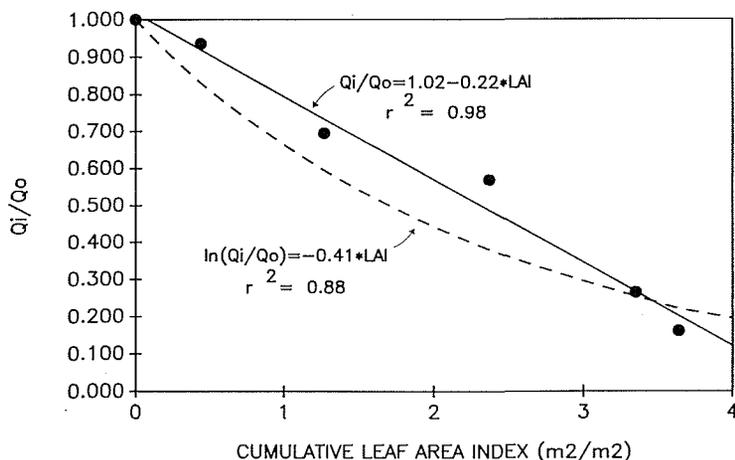


Figure 4. Regression equations relating Q_i/Q_o within the canopy to cumulative LAI. Actual data plotted as ●. Equations significant at $P < 0.05$.

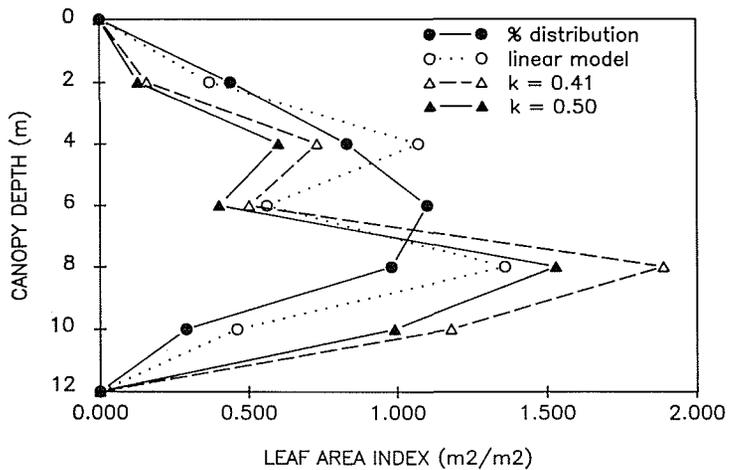


Figure 5. Comparison of vertical LAI distribution obtained from: (1) % distribution data, (2) linear model predictions, and (3) Beer-Lambert model predictions with $k = 0.41$ or $k = 0.50$.

result of a canopy gap not accounted for by the percent distribution data. Examination of the appropriate model for within canopy light attenuation will require a more extensive sample coupled with destructive sampling.

Although the linear model was most appropriate for describing the relationship between Q_i/Q_0 and cumulative LAI within the canopy, the linear model was used to predict stand LAI from ground level Q_i/Q_0 measurements. The relationship between Q_i/Q_0 and cumulative LAI from above canopy to ground level was linear; Q_i/Q_0 decreased from 18 m to ground level without an increase in cumulative LAI. This nonlinear relationship is influenced by PAR intercepted by branches and stem area below the live canopy.

Conclusions

Consistent with the results obtained by Pierce and Running (1988), the ceptometer predicted stand LAI within 9% of values determined from destructive sampling. In addition, the ceptometer was sensitive to changes in canopy PAR transmission resulting from new foliage production. Predicted stand LAI ranged from 3.2 in the dormant season to a maximum of 5.3 in late July. Converting PAR transmission collected at ground level to LAI requires determination of a proper k value which will depend on the significance of stem and branch shading. The increased accuracy of the ceptometer is a practical necessity for predicting LAI from ground level measurements. Our results indicated that the use of published k values in the Beer-Lambert Equation may result in erroneous LAI estimates if there is significant retention of dead branches and stem shading. An alternative approach is to use published canopy k estimates (e.g., 0.50) and modify the LAI predictions based on known surface areas of branches and stem below the forest canopy. The ceptometer was sensitive to seasonal changes in canopy PAR transmission.

PAR transmittance within the canopy; however, we found a linear relationship between Q_i/Q_0 measured within the canopy and cumulative LAI, as opposed to the exponential relationship assumed in the Beer-Lambert Equation.

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