Vertical leaf area distribution, light transmittance, and application of the Beer-Lambert Law in four mature hardwood stands in the southern Appalachians

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Abstract: We quantified stand leaf area index and vertical leaf area distribution, and developed canopy extinction coefficients *(k),* in four mature hardwood stands. Leaf area index, calculated from litter fall and specific leaf area ($cm^2 \cdot g^{-1}$), ranged from 4.3 to 5.4 $m^2 \cdot m^{-2}$. In three of the four stands, leaf area was distributed in the upper canopy. In the other stand, leaf area was uniformly distributed throughout the canopy. Variation in vertical leaf area distribution was related to the size and density of upper and lower canopy trees. Light transmittance through the canopies followed the Beer-Lambert Law, and *k* values ranged from 0.53 to 0.67. Application of these *k* values to an independent set of five hardwood stands with validation data for light transmittance and litter-fall leaf area index yielded variable results. For example, at $k = 0.53$, calculated leaf area index was within ±10% of litter-fall estimates for three of the five sites, but from -35 to +85% different for two other sites. Averaged across all validation sites, litter-fall leaf area index and Beer-Lambert leaf area index predictions were in much closer agreement (±7 to +15%).

Resume : Nous avons quantifié l'indice de surface foliaire du peuplement et la distribution verticale de la surface foliaire et nous avons développé des coefficients d'extinction du couvert *(k)* dans quatre peuplements feuillus matures. L'indice de surface foliaire, calcule a partir du depot de litiere et de la surface foliaire spécifique ($cm^2 \cdot g^{-1}$), variait de 4,3 a 5,4 $m^2 \cdot m^{-2}$. Dans trois des quatre peuplements, la surface foliaire etait concentrée dans la partie superieure du couvert. Dans l'autre peuplement, la surface foliaire etait distribuée uniformément dans tout le couvert. La variation dans la distribution verticale de la surface foliaire etait reliée a la dimension et a la densité des arbres dans la partie superieure et inférieure du couvert. La transmittance de la lumiere a travers le couvert suivait la loi de Beer-Lambert et les valeurs de *k* variaient de 0,53 a 0,67. L'application de ces valeurs de *k a* un groupe indépendant de cinq peuplements feuillus avec des données de validation pour la transmittance de la lumiere et I'indice de surface foliaire base sur le depot de litiere a produit des résultats variables. Pour une valcur de $k = 0,53$, par exemple, l'indice de surface foliaire calcule etait en dedans de ±10% des valeurs basées sur le depot de litiere pour trois des cinq peuplements, mais variait de −35 a +85% pour les deux autres peuplements. La valeur moyenne, pour tous les sites de validation, de I'indice de surface foliaire calcule a partir du depot de litiere correspondait beaucoup mieux (±7 a ±15%) a la valeur obtenue avec l'équation de Beer-Lambert.

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Introduction

Leaf area index (LAI, in $m^2 \cdot m^{-2}$) is a key measurement for understanding rates of energy and materials exchange between forest canopies and the atmosphere. Theoretical and empirical linkages between LAI and (I) light interception and productivity (e.g., Jarvis and Leverenz 1983; Linder 1985; Vose and Allen 1988), (2) deposition of atmospheric chemicals (Hosker and Lindberg 1982), (3) evapotranspiration

(Swank et al. 1988), and (4) site water balance (Grier and Running 1977) are well established. Vertical LAI distribution and subsequent variation in light transmittance within the canopy can also be an important regulator of canopy carbon gain (Russell et al. 1989), and characterization of LAI is required for many canopy models (e.g., Wang and Jarvis 1990).

Despite the recognized importance of LAI for understanding and (or) modeling many forest processes, information on stand LAI, vertical LAI distribution, and light transmittance are limited, especially for mature hardwood forest ecosystems. Methods used for measuring LAI in hardwood forests include destructive sampling (Valentine and Hilton 1977; Jurik et al. 1985), allometric equations (Monk et al. 1970; Jurik et al. 1985; McIntyre et al. 1990), litter fall (Madgwick and Olsen 1974; Jurik et al. 1985; Mclntyre et al. 1990; Chason et al. 1991), and light interception based techniques (Wang and Miller 1987; Mclntyre et al. 1990; Chason et al. 1991). These methods require assumptions and (or) additional measurements that may not be feasible in all situations. For example, allometric equations are typically site specific and often perform poorly when applied to other stands. Litter-fall approaches are slow and require estimates of specific leaf area (SLA, in $cm^2 \cdot g^{-1}$) to convert weight to area. Light interception based techniques require estimates of canopy light extinction coefficients *(k)* for direct-beam approaches (e.g., Beer-Lambert Law) and corrections for leaf overlap in diffuse-light approaches (Gower and Norman 1991). Vertical LAI and light transmittance are even more difficult to measure because accessing mature canopies is logistically difficult.

We used a combination of litter fall, canopy towers, line-intercept, and photosynthetically active radiation (PAR in $\mu mol \cdot m^{-2} \cdot s^{-1}$) measurements to quantify canopy attributes of four hardwood forests in the southern Appalachians of western North Carolina. Our objectives were (1) to quantify LAI, vertical LAI, and light transmittance in mature hardwood forest stands and (2) to determine variation in *k* among contrasting sites and forest types. In addition, we applied the *k* values to five independent hardwood stands with light transmittance and LAI data to assess the applicability of our *k* values to other stands.

Methods

Site descriptions

The study was conducted at the Coweeta Hydrologic Laboratory located in the southern Appalachians of western North Carolina. Four stands were selected to encompass a range of environmental conditions, density, basal area, and species composition (Table 1). Stands were located on control watersheds (Watersheds 2 and 27) that have had no direct human-caused disturbance since logging activities in the early 1990s. However, several natural disturbances, such as the chestnut blight, insect outbreaks, and drought-related mortality, have occurred since logging (Day et al. 1988; Clinton et al. 1993).

In the fall of 1991, towers were erected through the canopy of each stand. Care was taken to minimize canopy disturbance when placing the towers and corresponding guy wires. Towers ranged in height from 18 to 27 m. Vertical LAI and light penetration measurements were taken from the towers and litter-fall and mensurational measurements were taken from a 0.07-ha circular plot that circled each tower. Basal area, density, and tree height were measured for all tree species >6.4 cm DBH on each circular plot. Plot summaries are shown in Table 1.

Litter-fall LAI

Litter was collected in the spring, summer, and fall from four 0.18-m^2 traps systematically located (upslope, downslope, and two side slope positions) within 5 m of the tower location on each site. Leaf litter was sorted by species, dried at 60°C to a constant weight, and weighed to the nearest 0.01 g. Most litter mass (>75%) was collected in the late fall. A random subsample of three to eight leaves of those species representing 80 to 90% of total trap weight was selected for SLA determination. Leaves were rehydrated, placed in a plant press for 24 h, and measured with a leaf area meter (LI-COR 3000, Lincoln, Nebr.). We tested for differences in species-specific SLA among sites and found no differences (analysis of variance; a = 0.05). Therefore, we averaged species-specific SLA values across sites. SLA values among species ranged from 138 to 305 $cm^2 \cdot g^{-1}$. To calculate leaf area, species- and season-specific SLA values were multiplied by their corresponding litter weights. Average site SLA values were used for the remaining species. LAI was determined by summing leaf area values for all species and dividing by trap area. Because traps were clustered around the towers, LAI estimates derived from the litter traps were most representative of the area around the towers and not the entire 0.07-ha plot.

Vertical LAI

In July 1993, we used the line-intercept technique (MacArthur and MacArthur 1961) in combination with litter-fall LAI estimates to estimate vertical LAI. We chose this technique because destructive sampling was not possible (i.e., leaves accessed from the towers were also used in physiological studies) and modified versions of this technique have been previously used to estimate vertical LAI profiles in hardwood canopies (Aber 1979; Hedman and Binkley 1988). A vertical line (string) with a plumb bob attached to the bottom was lowered from the top of the canopy to the forest floor. The line was positioned approximately 1 m horizontally from the tower. Leaf contacts were counted at 1-m intervals and recorded by species. This procedure was repeated six times at each tower. The position of the first line was randomly determined; the next five were distributed in a circular fashion at ≈60° intervals. Values for the six measurements were averaged for each 1-m interval. LAI for each 1-m interval was calculated as the number of contacts at level *i*/total number of contacts X litter-fall LAI. We used litter-fall LAI as our measure of stand LAI because the line-intercept technique provides accurate measures of the relative distribution of LAI but inaccurate estimates of total stand LAI (Aber 1978).

Light transmittance

PAR at 2-m canopy height intervals was measured with a Sunfleck ceptometer (Decagon Inc., Pullman, Wash.). The ceptometer measures and calculates average PAR incident

Table 1. Summary of stand and site characteristics.

Parameter	Site			
	WS 2L	WS 2H	WS 27L	WS 27H
Tower height (m)	24.0	17.8	26.8	21.0
Elevation (m)	740	840	1070	1430
Aspect	E	SE	E	N
Slope (%)	52	29	24	35
Trees/ha	780	960	765	405
Basal area ($m^2 \cdot ha^{-1}$)	33.5	21.4	36.2	32.1
Mean DBH (cm)	19.7	15.3	21.3	27.3
Growing season precipitation (mm)	950	950	1250	1300
Litter-fall LAI ($m^2 \cdot m^{-2}$)	4.3	4.5	4.7	5.4

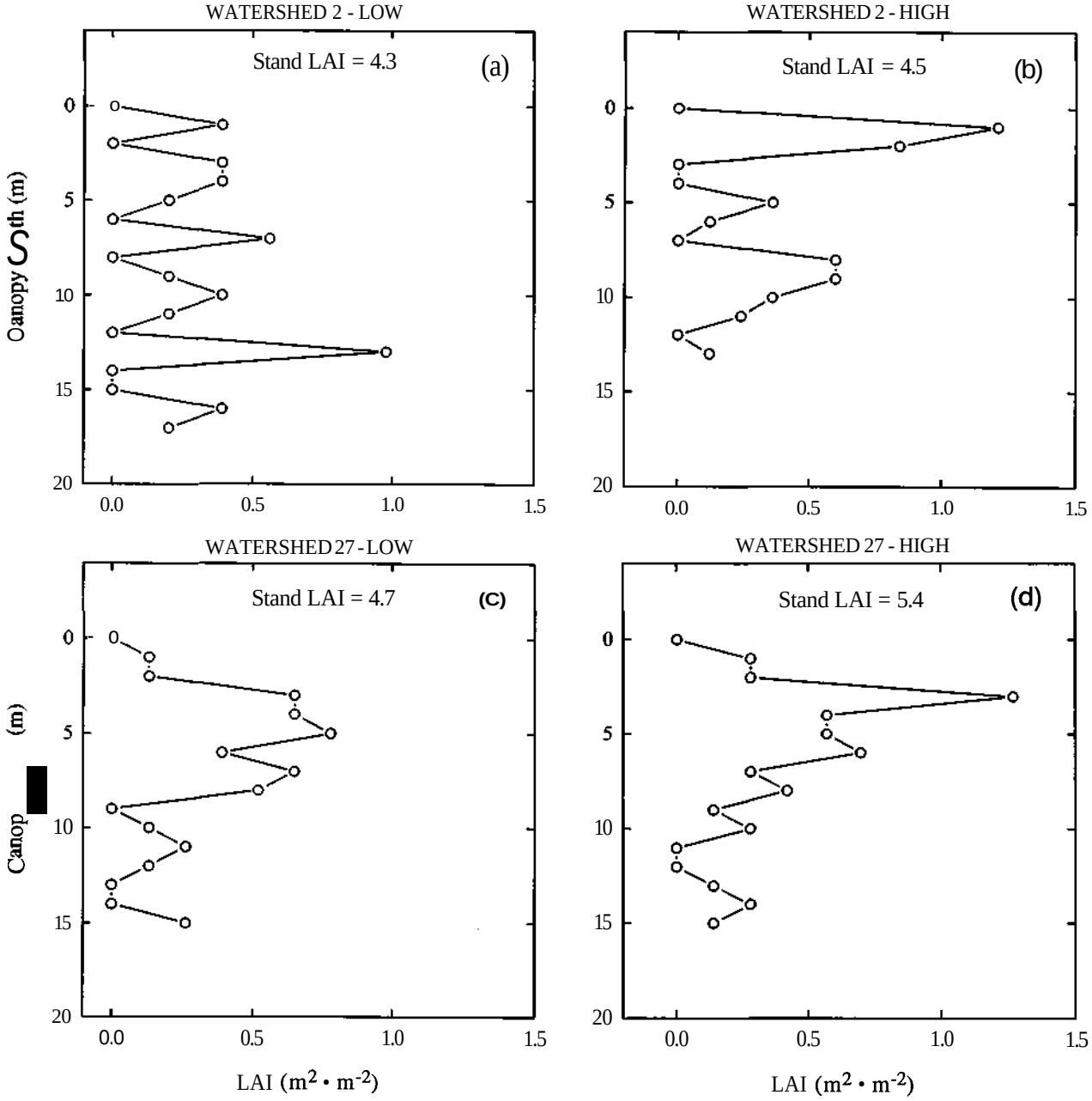
Table 2. Comparison of litter-fall LAI and LAI predicted with the Beer-Lambert Law on five sites.

Site	Elevation (m)	Aspect	Major species	Litter-fall LAI	Beer-Lambert Law LAI		
					k = 0.53	k = 0.62	k = 0.67
1	990	S	*Q. velutina* *Q. prinus* *A. rubrum* *T. canadensis* *R. maximum*	5.8	6.0 (+3)	5.2 (−10)	4.8 (−17)
2	1184	SW	*Q. alba* *Q. rubrum* *Q. prinus* *A. pensylvanicum* *C. florida*	4.5	8.1 (+80)	6.9 (+53)	6.4 (+42)
3	745	N	*Q. prinus* *Q. velutina* *L. tulipifera* *T. canadensis* *A. rubrum*	6.2	4.0 (-35)	3.4 (-45)	3.2 (-48)
4	991	N	*Q. velutina* *Q. prinus* *N. sylvatica* *A. pensylvanicum* *A. rubrum*	7.3	7.7 (+5)	6.5 (-11)	6.1 (-16)
5	1372	E	*Q. rubrum* *A. saccharum* *B. lenta* *B. lutea* *A. pensylvanicum*	3.9	3.9 (0)	3.4 (-13)	3.1 (-21)
Mean±SE				5.5±0.6	5.9±0.9	5.1±0.8	4.7±0.7

Note: Numbers in parentheses are percent deviation of Beer-Lambert LAI values from litter-fall LAI estimates.

on 80 sensors located at 1-cm intervals along a narrow, 80-cm probe. Four measurements were taken in a circular fashion (≈ 90° intervals) at each height interval and averaged to provide a mean PAR value for each 2-m interval. Average maximum sun angle (solar noon) in June and July in western North Carolina is approximately 75° (Smithsonian Institution 1951). Because sun angle also varies during the day, we sampled between 11:00 and 14:00. Variation in sun angle during this period is less than 10% (Smithsonian Institution 1951). Measurements were taken on clear days, and the first tower measurement (i.e., above canopy) was used as the total incoming PAR value (Q_o).

Fig. 1. Vertical distribution of total stand leaf area determined with the line-intercept method and litter fall. Zero represents the top of the canopy.



Canopy extinction coefficients

Extinction coefficients *(k)* were determined for each stand using the Beer-Lambert equation, cumulative LAI (summed over 2-m intervals) through the canopy, and vertical PAR transmittance (2-m intervals). Linear regression (no intercept model) was used to estimate *k* with the following function:

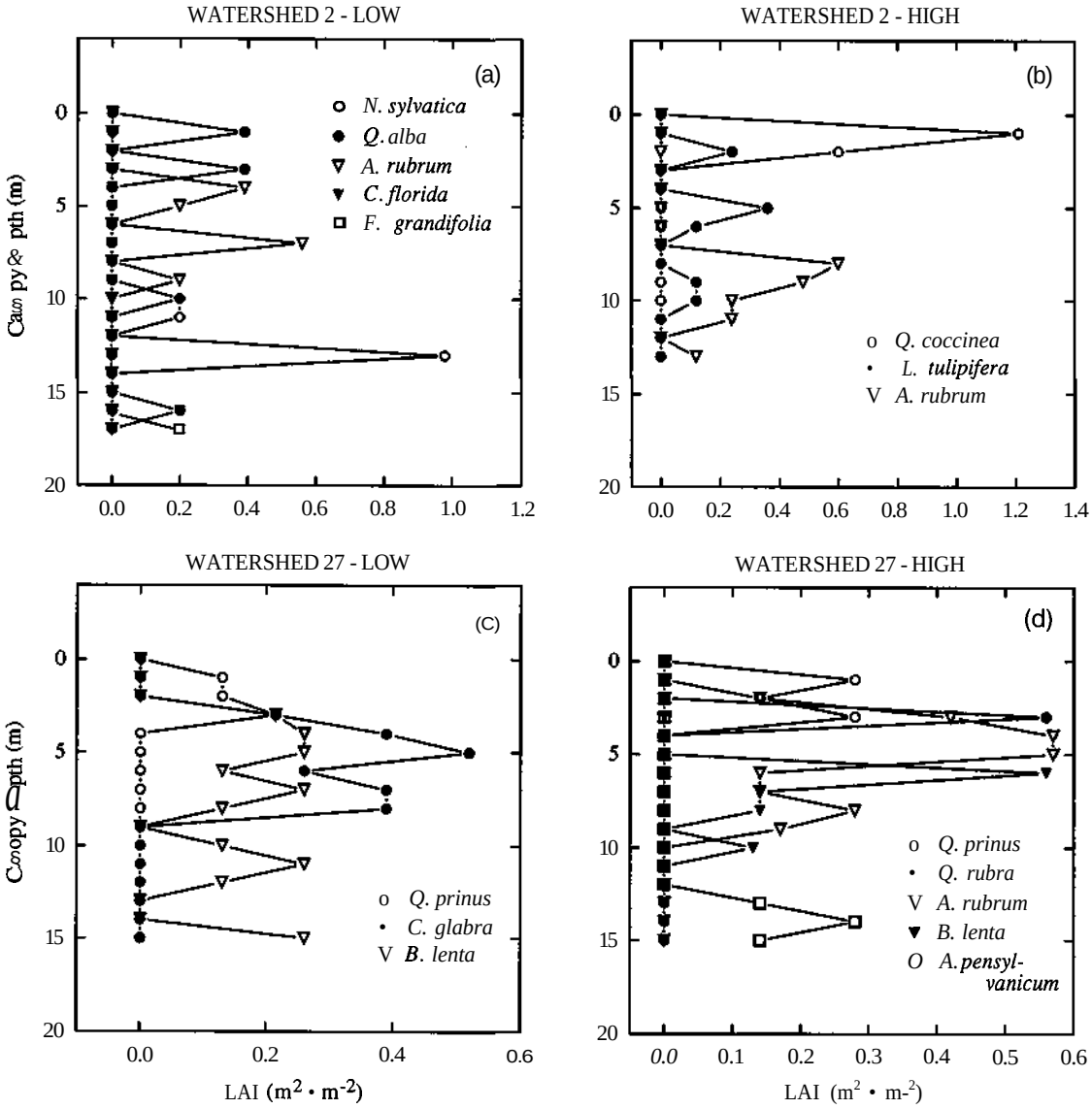
$$\ln\left(\frac{Q_i}{Q_o}\right) = k(\mathrm{LAI}_i)$$

where Q_i/Q_o is the fraction of PAR transmitted at canopy depth *i*, Q_i is PAR transmittance at canopy depth *i*, Q_o is total incoming PAR, *k* is the canopy extinction coefficient, and LAI_i is cumulative LAI at canopy depth *i*.

This calculation assumes that foliage is randomly distributed in the canopy and that leaf inclination angles are spherically distributed in space. However, the Beer-Lambert equation is fairly insensitive to violations of these assumptions (Jarvis and Leverenz 1983; Pierce and Running 1988).

We validated the application of the Beer-Lambert Law and *k* values with an independent data set of light transmittance and litter-fall LAI. Canopy transmittance was measured with a Sunfleck ceptometer in June 1989 at 10 randomly located ground-level sample points in each of five 0.05-ha plots. The five sites represented a range

Fig. 2. Vertical distribution of individual species leaf area determined with the line-intercept method and litter fall. Zero represents the top of the canopy.



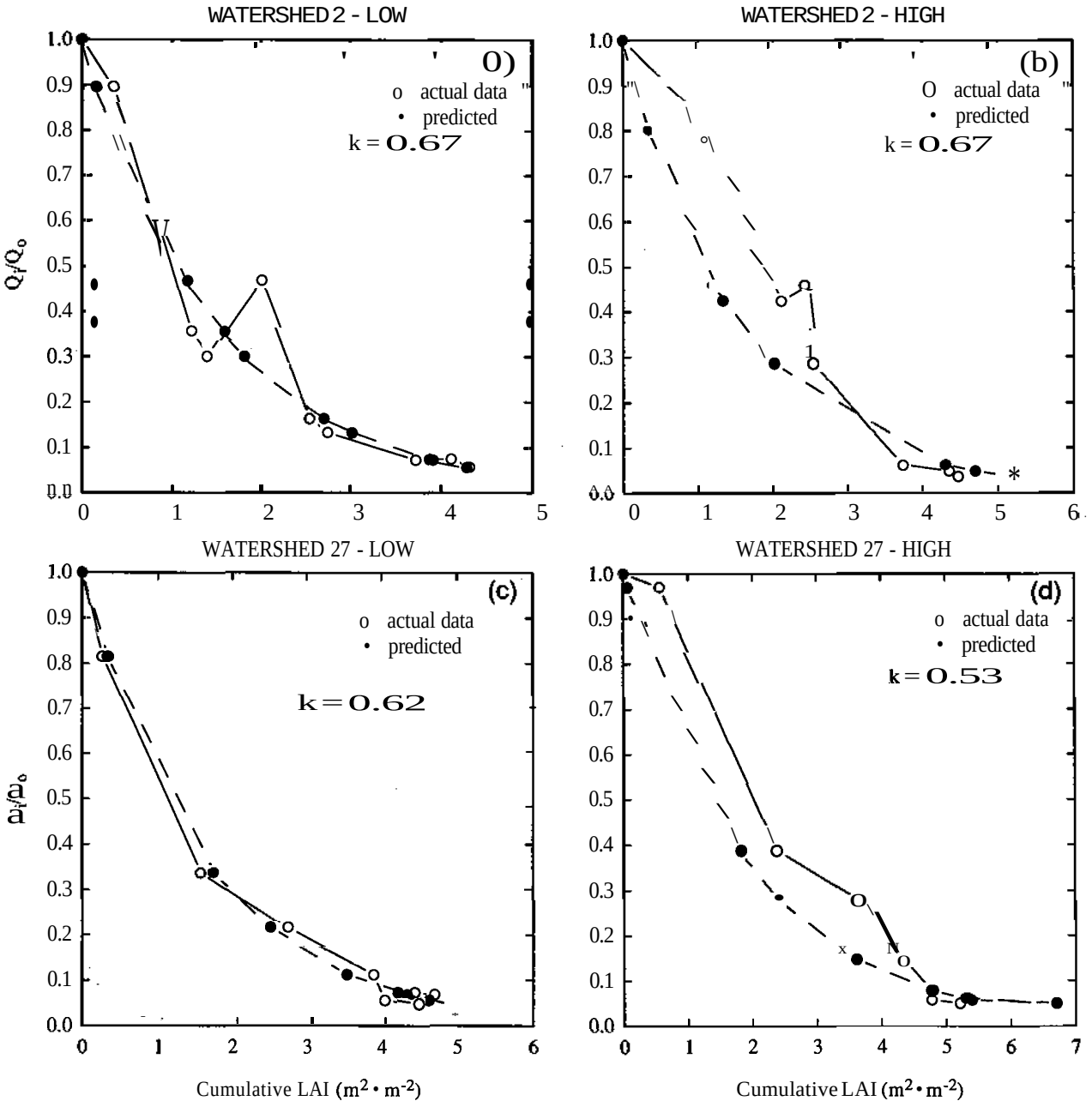
of aspects, elevations, and species composition (Table 2). Measurements were taken between 11:00 and 13:00. Each sample point Q_i measurement represented the mean of 10 samples taken in a circular fashion at ≈36° intervals. Incoming PAR (Q_o) was measured in open areas before and after Q_i measurements were taken at each site, and the average of these two measurements was used for Q_o in subsequent calculations. Litter fall was collected from four randomly located 0.41-m^2 traps at each site. Leaf area index was calculated using leaf litter mass and species-specific SLA values.

Results and discussion

Stand LAI

Stand LAI ranged from 4.3 to 5.4 $m^2 \cdot m^{-2}$ (Table 1). The greatest LAI (5.4 $m^2 \cdot m^{-2}$) was observed in the high-elevation northern hardwood stand, where *Quercus rubra* L., *Acer rubrum* L., and *Quercus prinus L.* composed 74% of the total stand LAI. The lowest LAI (4.3 $m^2 \cdot m^{-2}$) was observed in the low-elevation mixed oak stand, where *A. rubrum, Carya glabra* (Mill.) Sweet, *Q. prinus,* and *Quercus coccinea* Muenchh. composed 71% of the total stand LAI. These values are within the range of LAI values reported for other eastern deciduous forests (Aber 1979; Hedman and Binkley 1988; Monk and Day 1988; Chason et al. 1991; Ellsworth and Reich 1993). While general relationships among LAI and stand structure characteristics have been shown in other studies (e.g., Gresham 1982), no clear relationships (based on scatterplots) between LAI and other stand attributes (Table 1) were found in our study. We know of no studies examining stand attributes and LAI in hardwoods in the southeast United States; however, shorter term assessments of LAI recovery following clear-cutting in the southern Appalachians show that LAI approaches near precut levels within 10 to 15 years (Boring et al. 1988).

Fig. 3. Canopy light transmittance vs. cumulative LAI. Broken lines and solid symbols represent predicted transmittance with the Beer-Lambert Law. Solid lines and open symbols are actual canopy transmittance.



In our study, the range in LAI and other stand structure characteristics (e.g., basal area) may have been too small to show any relationships.

Vertical distribution of LAI

There was variation in the vertical distribution of LAI among the four stands (Figs. *la-Id).* Three stands (WS 27H, WS 2H, WS 27L) had a large proportion (50 to 56%) of LAI distributed in the upper third of the canopy, while WS 2L had a nearly even LAI distribution, with the exception of a high LAI value at 13-m crown depth. Hedman and Binkley (1988) found even greater variation including upward, downward, and uniform vertical LAI distributions in hardwood stands in the piedmont region of North Carolina. The vertical LAI distributions for each stand in our study were most likely determined by stand structure and species composition. For example, WS 27H had large trees (mean DBH = 27.3 cm), which contributed to the high LAI in the upper canopy (Figs. *2a–2d)* and only one species, *Acer pensylvanicum* L., occurred in the lower canopy (>10-m canopy depth). In contrast, WS 2L had smaller trees (mean DBH = 19.7 cm), and three species *(Nyssa sylvatica* Marsh., *Cornus florida* L., *Fraxinus americana* L.) occurred in the lower canopy (Figs. *la-Id).* Although litter-fall LAI varied from 4.3 to 5.4 $m^2 \cdot m^{-2}$ among the sites, light in the lower canopy was comparable

(5-10% of incoming PAR) among the four stands (Figs. 3*a*-3*d*). Therefore, the larger number of species and greater LAI in lower canopy positions on WS 2L (which also had the lowest LAI) are not a result of greater light availability.

The variation in vertical LAI distribution in our study and others (e.g., Aber et al. 1982; Hedman and Binkley 1988; McIntyre et al. 1990) contrasts with patterns observed for coniferous stands. With conifers, stands typically progress through stages of downward, normal, and upward vertical LAI distributions as the stands develop from open to closed canopy conditions (Schreuder and Swank 1974; Vose 1988; Vose et al. 1994). Characterizing vertical LAI distribution in mixed-species hardwood stands is much more difficult because of the potential contribution of shade-tolerant species or gap-phase succession in the lower canopy. The occurrence of these species is related to multiple factors, such as disturbance history, stand age (Aber 1979), and site quality (Aber et al. 1982).

Canopy light transmittance and *k*

Canopy light transmittance followed the Beer-Lambert Law reasonably well (Figs. 3*a*–3*d*). Regressions relating cumulative LAI to $\ln(Q_i/Q_o)$ were highly significant ($P < 0.0001$), and *k* values ranged from 0.53 to 0.67, with a mean of 0.62. This mean is in the upper range of *k* values reported for a variety of hardwood forests (Jarvis and Leverenz 1983; Baldocchi et al. 1985). We applied the Beer-Lambert Law and the mean and range of *k* values to an independent data set of canopy transmittance and litter-fall LAI collected from five diverse sites in the Coweeta basin (Table 2). Results showed that LAI predictions at individual sites were often poor (>10% deviation). The lower *k* (0.53) predicted three stand LAIs within 10%, but using the mean *k* and the highest *k* resulted in poor agreement between predicted and litter-fall LAI values. The worst predictions (>30% deviation) occurred for site 2, a high-elevation stand, and site 3, a low-elevation stand. Averaged across all sites, litter-fall LAI and Beer-Lambert LAI predictions were in much closer agreement (7 to 15%).

There are several potential factors contributing to the site specificity in *k* we observed. For example, in mixed stands, variation in species composition and vertical distribution could influence canopy architecture through differences in the arrangement of foliage (Gholz et al. 1991) and the amount and distribution of stem and branch area (Norman and Jarvis 1974). These factors are equally important in pure stands. For example, in lodgepole pine (*Pinus contorta* var. *latifolia*)stands, Smith et al. (1991) found poor agreement between LAI predicted with the Beer-Lambert Law and an average *k* of 0.52 versus LAI estimated with allometric equations. They attributed most of the inaccuracy to variation in canopy architecture and stand structure among stands. These results indicate that even in pure stands or stands with similar species composition, differences in canopy architecture due to stand structure (e.g., density, basal area, etc.) can result in substantial variation in *k*.

Similar to the conclusions of Smith et al. (1991) in pure stands, the results of our study indicate that site-specific estimates of *k* are required for accurate LAI predictions in mixed hardwood stands. This implication limits the utility of the Beer-Lambert Law for estimating stand-specific LAI because determining *k* is not a trivial task. Although we were unable to establish relationships between *k* and stand attributes in our study, a more extensive and intensive study might reveal predictable relationships. In the meantime, our results indicate that the most appropriate application of the Beer-Lambert Law and nonspecific *k* values is for determining average LAI values across several sites, such as watershed scale estimates.

Summary and conclusions

Stand LAI varied from 4.3 to 5.4 $m^2 \cdot m^{-2}$ and >50% of LAI was distributed in the upper third of the canopy on three of the four stands quantified. The other stand had a more uniform LAI distribution that was related to the influence of several understory trees. Light transmittance through the canopies followed the Beer-Lambert Law, and *k* values ranged from 0.53 to 0.67, with a mean of 0.62. Variable results were obtained with these *k* values in estimating stand LAI with an independent set of ground-level Q_i measurements and litter-fall LAI estimates. Results indicated that site- and stand-specific *k* values may be required to accurately estimate LAI at a given location; however, predictions were more accurate when averaged over several stands.

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