

Leaf area index of an old-growth Douglas-fir forest estimated from direct structural measurements in the canopy

Sean C. Thomas and William E. Winner

Abstract: Leaf area index (LAI) in old-growth Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) forests exceeds that of any other forest ecosystem by some estimates; however, LAI determinations in coniferous forests have generally been indirect, involving extrapolations of patterns observed in younger stands. Aided by a 75-m construction crane for canopy access, we used a vertical line-intercept method to estimate LAI for a ≥450-year-old Douglas-fir – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest in southwestern Washington state. LAI was calculated as the product of foliage contact frequency and an “extinction coefficient” accounting for foliage angular distribution, geometry, and the ratio of “interceptable” to total leaf area. LAI estimates were 9.3 ± 2.1 (estimate ± 95% confidence interval), 8.5 ± 2.2 , and 8.2 ± 1.8 in 1997, 1998, and 1999, respectively, or 8.6 ± 1.1 pooled across years. Understory vegetation, including foliage of woody stems <5 cm diameter, represented 20% of this total. Sample points in which Douglas-fir was dominant had a higher total LAI than points dominated by western hemlock, including a higher LAI of understory vegetation. Our results do not support the contention that old-growth Douglas-fir – western hemlock forests maintain an appreciably higher LAI than do other forest ecosystems. Moreover, LAI in very old stands may decline as western hemlock replaces Douglas-fir through the course of succession.

Résumé : Selon certains estimés, l'indice de surface foliaire (LAI) dans les vieilles forêts de douglas de Menzies (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) dépasse celui de n'importe quel autre écosystème forestier. Cependant, la détermination de la valeur de LAI dans les forêts de conifères a généralement été faite de façon indirecte en extrapolant les patrons observés dans de plus jeunes peuplements. En ayant recours à une grue de chantier de construction de 75 m pour atteindre la canopée, les auteurs ont utilisé une méthode basée sur l'interception d'une ligne verticale pour déterminer la valeur de LAI dans une forêt de douglas de Menzies et de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) âgée de plus de 450 ans et située dans le sud-ouest de l'État de Washington. La valeur de LAI a été calculée comme étant le produit de la fréquence de contact avec le feuillage par un coefficient d'extinction qui tient compte de la distribution angulaire et de la géométrie du feuillage ainsi que du rapport de la surface foliaire qui peut être interceptée sur la surface foliaire totale. Les estimés de la valeur de LAI étaient respectivement de $9,3 \pm 2,1$, $8,5 \pm 2,2$ et $8,2 \pm 1,8$ pour 1997, 1998 et 1999 ou de $8,6 \pm 1,1$ pour l'ensemble des années (l'intervalle de confiance est au niveau de 95%). La végétation de sous-bois, incluant le feuillage des tiges ligneuses de moins de 5 cm de diamètre, représentait 20% du total. Les points d'échantillonnage où le douglas était dominant avaient une valeur de LAI plus grande que ceux où la pruche de l'Ouest dominait, incluant une valeur de LAI plus élevée pour la végétation de sous-bois. Nos résultats ne supportent pas l'affirmation voulant que les vieilles forêts de douglas de Menzies et de pruche de l'Ouest aient une valeur de LAI plus élevée que les autres écosystèmes forestiers. De plus, dans les très vieux peuplements la valeur de LAI peut diminuer à mesure que la pruche de l'Ouest remplace le douglas de Menzies dans le cours de la succession.

[Traduit par la Rédaction]

Introduction

Leaf area index (LAI), defined as the projected area of foliage per unit ground area, is the most common and, argu-

ably, most useful comparative measure of foliage quantity (Watson 1947; Parker 1995; Kram 1998). Accurate measurements of forest LAI are of fundamental importance as a basis for estimating the exchange of carbon, water, nutrients, and light at the ecosystem level. LAI is thus a critical parameter in physiology-based models of forest responses to global environmental change (e.g., Nemani and Running 1989; Potter et al. 1993; Kimball et al. 1997) and also one of the main links between remote sensing data and forest ecosystem function (e.g., Spanner et al. 1994; Chen and Cihlar 1996; Franklin et al. 1997; White et al. 1997; Lefsky et al. 1999). However, reliable “ground-truth” estimates of LAI have presented a long-standing empirical challenge in tall forest systems that possess evergreen phenology (Kira 1978;

Received April 17, 2000. Accepted September 15, 2000.
Published on the NRC Research Press website on
November 25, 2000.

S.C. Thomas¹ and W.E. Winner. Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331-2902, U.S.A.

¹Corresponding author. Present address: Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, ON M5S 3B3, Canada. e-mail: sc.thomas@utoronto.ca

Alexandre 1981; Marshall and Waring 1986; Turner et al. 2000).

The first-published estimates of LAI for old-growth forests dominated by Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) ranged from ~10 to 22 (Gholz et al. 1976; Grier and Running 1977; Waring et al. 1978; Franklin and Waring 1981; Gholz 1982). Such values are greater than those reported for any other forest system, including other coniferous forests (Jarvis and Leverenz 1983; Gower and Norman 1991; Jack and Long 1991; Chen 1996), temperate deciduous forests (Whittaker and Woodwell 1968; Kira, et al. 1969; Parker et al. 1989; Tokar 1997; Cutini et al. 1998; Kram 1998), and tropical evergreen forests (Ogawa et al. 1965; Kato et al. 1978; Kira 1978). Only from coast redwood forests dominated by *Sequoia sempervirens* (D. Don) Endl. have similarly high LAI values been reported (Westman and Whittaker 1975). Some care must be taken in comparing these LAI values with others reported in the literature, since several definitions of LAI have been used for conifer species possessing non-flat leaves (Chen and Black 1992; Barclay and Goodman 2000). Here we take LAI to refer specifically to the vertically projected area of leaves arranged horizontally per unit ground area, following the original definition of Watson (1947). The most commonly used alternative definition is half of the total external surface area of leaves per unit ground area (e.g., Chen and Black 1992), which we denote HTLAI. Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) have relatively flat needles, so the difference between HTLAI and LAI is not very large, with estimated conversion factors (HTLAI/LAI) ranging from 1.07 to 1.19 (Gholz et al. 1976; Barclay and Goodman 2000).

The exceptionally high LAI values originally reported for old-growth Douglas-fir forests were based on simple extrapolations of allometric relationships between leaf area and stem diameter ultimately derived from measurements in younger stands. Marshall and Waring (1986) found that estimates based on allometric relationships between sapwood area and leaf area yielded LAI values more similar to those reported from other coniferous forests (e.g., ~8.3 for trees in a 450-year-old Douglas-fir – western hemlock stand in the H.J. Andrews Experimental Forest, Oregon). Sapwood-based estimates for the Andrews site were also in relatively close agreement with indirect analyses involving light interception analyzed via the Beer–Lambert relationship, and with analyses of litter fall and leaf demographic data (Marshall and Waring 1986). However, even the most recently published LAI values for mature and old-growth Douglas-fir stands based on sapwood – leaf area allometric calculations range from 4.2 to 14.0 (Turner et al. 2000), with most of this variation attributable to the specific algorithm used.

To date, all published estimates of LAI for old-growth forests in the Pacific Northwest region have involved some element of extrapolation of relationships observed in younger stands or other assumptions not directly supported by on-site data. In particular, extrapolation of allometric data from young stands is suspect in that such an approach neglects ontogenetic changes in tree morphology and physiology (Yoder et al. 1994; Thomas and Ickes 1995; Thomas and Bazzaz 1999). In this regard, previous studies of deciduous forests have suggested a gradual decline in LAI with stand

age through the latter course of stand development (Ford and Newbould 1971; Kram 1998). Applications of the Beer–Lambert relationship or of gap-fraction calculations generally involve assumptions of random spatial distribution of foliage and a spherical or ellipsoidal distribution of leaf angles (Campbell and Norman 1989; Gower and Norman 1991; Huston et al. 1991; Martens et al. 1993; but see Chen and Cihlar 1995; Van Gardingen et al. 1999). Conifers typically exhibit highly clumped foliage, and thus, simple inversion of optical data results in a substantial underestimate of LAI values in conifer stands (Smith et al. 1993; deBlonde et al. 1994; Fassnacht et al. 1994; Stenberg et al. 1995; Sampson and Allen 1995; Chen 1996; Küßner and Mosandl 2000). Canopies of old-growth systems are likely to be extreme in this regard, showing foliage clumping at various spatial scales (Van Pelt and North 1996; Parker 1997).

In the present study we estimate LAI for an old-growth Douglas-fir – western hemlock forest employing a vertical line-intercept method similar to that used in low-stature vegetation such as grasslands and deserts (e.g., Warren-Wilson 1965; Groeneveld 1997). Access to the canopy was provided by a large construction crane situated in an undisturbed stand. Two main modifications were necessary to adapt the line-intercept approach for coniferous forests. Firstly, intercepts were estimated for branchlets, rather than individual needles, to insure that the linear dimensions of canopy elements were much larger than that of the vertical line (Warren-Wilson 1963). Secondly, calculations accounted for both branchlet geometry and for the ratio of the projected area of space occupied by branchlets to projected needle area obtain estimate the ratio of contact frequency to LAI. Our approach enabled formal randomization of observations within the stand, and also direct, on-site determination of all geometric and morphological parameters used in the calculations.

We addressed the following questions in this study. (i) Is the vertical line intercept described a tractable method for estimating LAI in tall coniferous forests? (ii) How do LAI estimates based on this method vary between years, and how do they compare to previously published values for old-growth Douglas-fir stands? (iii) What is the relative contribution of canopy and understory species to LAI at the site? (iv) How does the amount and species diversity of local LAI vary among canopy tree species?

Materials and methods

Study site and line-intercept measurements

The study was conducted at the Wind River Canopy Crane site, located within the Thornton T. Munger Research Natural Area of the Gifford Pinchot National Forest (45°49'N, 121°58'W) in southwestern Washington state. The site is situated in the Wind River valley at an elevation of 355 m, on relatively nutrient-poor, coarse-textured soils developing over a 2–3 m deep layer of volcanic ejecta (Franklin et al. 1972). Annual precipitation averages 2500 mm, and mean annual temperature is 8.7°C. On the basis of tree ring counts near the site, the largest trees in the stand are ~450 years old, with Douglas-fir and western hemlock dominant, with western redcedar (*Thuja plicata* Donn.) also an important element (DeBell and Franklin 1987). The tallest Douglas-fir individuals reach ~65 m in height at the site (Ishii et al. 2000). Other canopy tree species present include *Abies grandis* (Dougl.) Forbes, *Abies*

procera Rehd., and *Pinus monticola* Dougl., but these make up less than 2% of total basal area (and were not encountered during line-intercept sampling). Understory tree species include abundant pacific yew (*Taxus brevifolia* Nutt.) and Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), which rarely attains heights >10 m at the site. Dominant species of the shrub and herb layers include salal (*Gaultheria shallon* Pursh), vine maple (*Acer circinatum* Pursh), Oregon-grape (*Berberis nervosa* Pursh), and vanillaleaf (*Achlys triphylla* (Smith) DC). Botanical nomenclature follows Hitchcock and Cronquist (1973).

A Liebherr 550 HC tower crane (Morrow Crane Inc., Salem, Oreg.), with jib height of 74.5 m and range of 87 m (crane circle area 2.3 ha) was used to access points above and within the forest canopy. Sampled points for vertical transects were chosen as a Poisson–Poisson spatial point process (Diggle 1983) within the crane circle. A list of random points was generated as Cartesian coordinates, and then transformed into azimuth and radius values corresponding to the crane operator's output for "swing" and "trolley," respectively. The personnel platform ("gondola") was positioned at a given coordinate and lowered to a position within 2 m of the canopy at that point. A vertical line was then lowered from a fixed position on the gondola. To minimize line thickness while retaining sufficient line strength, we used one edge of a fiber glass measuring tape (thickness <0.10 mm) bearing a lead weight. The line was slowly lowered and each intercept point ("contact") was checked following cessation of line sway and branch movement. A contact was scored where a horizontal layer of foliage overlapped the specified edge of the tape; only intercepts for vascular plant foliage (not branches) were tallied. For each contact we noted species and canopy layer ("upper canopy," "midcanopy," "lower canopy," and "understory"). The latter classification was based on a subjective evaluation of foliage morphology, with absolute heights varying by species, tree height, and degree of crown exposure. We elected to use this subjective scheme, rather than absolute height in the canopy, to better match intercept counts with measured morphological characteristics of foliage. Contacts which were considered uncertain due to difficulties in visibility, line sway, or interference from branches were noted. All vertical intercept measurements were obtained during periods of low air movement. Three rounds of line-intercept sampling, each involving 30 line drops were conducted on Sept. 9, 1997; July 18, 1998; and Sept. 25, 1999.

Using observers with binoculars positioned both in the crane gondola and on the forest floor, it was possible to obtain accurate counts of the number of vertical line intercepts with foliage layers in the manner described above. However, in some cases a contact could represent more than one branchlet, such as when the line contacted a point where two or more branchlets intersected. It was not possible to accurately resolve these instances of multiple contacts from a distance nor was it possible to position the crane gondola sufficiently close to all contact positions to accurately make this distinction. We therefore conducted an additional sampling exercise to estimate the average number of branchlet contacts per observed contact with a horizontal foliage layer. At the same points used for collection of canopy foliage, a vertically oriented laser was positioned at randomly selected points above an accessible layer of foliage. The actual number of contacts per observable contact was then determined for a set of 200–250 points per foliage layer for the dominant canopy tree species. This data set was later augmented by additional measurements of this type on branches taken from recently fallen trees at the site.

Morphological measurements

We sampled additional foliage characteristics necessary for LAI calculations at selected intervals from September 1996 through June 1999. For canopy foliage, representative locations were chosen for upper, middle, and lower canopy positions of two or three

representative *Pseudotsuga menziesii* and *Tsuga heterophylla* trees, with upper and lower canopy samples taken for *Thuja plicata*, and lower canopy (only) for *Taxus brevifolia* and *Abies amabilis*. Foliage at a given location was chosen by enumerating all accessible branches, and then selecting a randomly determined set of 5–10 branches for measurements. Branchlet angle (deviation from a horizontal plane) was measured to the nearest 1° using a clinometer (Suunto MC-1, Suunto, Espoo, Finland), internode length (*L*) was measured to the nearest 1 mm, and the age-class of each measured internode was noted. In addition, destructive samples (collected in conjunction with photosynthesis measurements for major tree species) were used to measure total leaf area, and branchlet width (*W*) and height (*H*), measured normal to the growing axis to the edge of the furthest projecting needles. The "interceptable" area of each horizontally positioned branchlet was estimated as the area of an ellipse with major axis length = 0.5*L*, and minor axis length = 0.5*W*. Foliage was harvested and stored at 0°C prior to measurement, and digital images were collected to determine total (one-sided) leaf area for each branchlet. The ratio of "interceptable" to total leaf area (ITAR) was calculated separately for each sample (note that ITAR will typically be greater than the silhouette to total leaf area ratio (STAR) commonly measured in studies of conifer functional morphology, e.g., Stenberg et al. 1995). Images of horizontally displayed branchlets and of detached leaves were collected with either a Connectix QuickCam or a Umax Astra 600S flatbed scanner, and analyzed using NIH Image version 1.59. We did not correct for three-dimensional needle geometry in estimating total needle area of each sampled branchlet, except as indicated to calculate whole-stand HTLAI. For this purpose, the following constants were used to convert "projected" needle area to "half total" needle area: 1.18 for *P. menziesii*, 1.07 for *T. heterophylla*, 1.50 for *T. plicata*, 1.07 for *T. brevifolia*, and 1.16 for *A. amabilis* (Gholz et al. 1976).

LAI estimation: procedures and assumptions

The area index of a given canopy element, *L_i*, is related to the contact frequency of vertical linear transects through the canopy by

$$[1] \quad L_i = \frac{N_i}{K_i}$$

where *N_i* is the contract frequency of the *i*th canopy element; *K_i*, the "extinction coefficient," is defined as the ratio of the total projected area of canopy elements (in their original orientation) on a horizontal plane to the total projected area of the elements each rotated to a horizontal orientation (Warren-Wilson 1965; Anderson 1966; Campbell and Norman 1989). The subscript *i* denotes a given class of canopy elements. The extinction coefficient, *K_i*, for "flat" canopy elements (having one dimension much smaller than others, as in many plant leaves), is entirely a function of the angular distribution of these elements (Campbell and Norman 1989). However, *K_i* for canopy elements that are not flat will be determined by both the angular distribution and three-dimensional geometry of the elements.

In a companion paper we describe a "rotated ellipsoidal distribution" model used here to empirically estimate leaf and branchlet angle distributions (Thomas and Winner 2000). The model corresponds geometrically to an ellipsoid with canopy elements normal to the surface and provided a better description of observed foliage angle distributions than did the commonly used "ellipsoidal distribution" of Campbell (1986, 1990). The probability distribution function for the rotated ellipsoidal distribution is

$$[2] \quad g(\theta) = \frac{2\chi^3 \cos \theta}{\Lambda(\sin^2 \theta + \chi^2 \cos^2 \theta)^2}$$

Table 1. Morphological characteristics for dominant canopy and understory species used in deriving LAI estimates at the Wind River Canopy Crane site.

Species	Height	Branch overlap	Mean angle ($^{\circ}$)	X'	ITAR	L/W	H/W	K_i
Canopy trees								
<i>Pseudotsuga menziesii</i>	Upper	1.31	29	0.793	0.594±0.229	2.484±0.927	0.963	0.477
	Middle	1.26	41	1.328	0.697±0.189	2.330±0.702	0.940	0.525
	Lower	1.22	34	1.019	0.792±0.152	2.082±0.397	0.676	0.628
<i>Tsuga heterophylla</i>	Upper	1.33	36	1.073	0.908±0.273	1.411±0.317	0.366	0.630
	Middle	1.25	25	0.657	1.232±0.327	1.446±0.301	0.327	1.015
	Lower	1.17	33	0.951	1.231±0.359	1.675±0.654	0.244	0.917
<i>Thuja plicata</i>	Upper	1.10	56	2.402	1.363	—	—	0.508
	Middle	(1.15)	(58)	(2.601)	1.268	—	—	0.495
	Lower	1.20	60	2.790	1.155	—	—	0.481
Subcanopy trees								
<i>Taxus brevifolia</i>	Lower	~1.00	14	0.33	1.292±0.201	1.587±0.117	0.050	1.619
<i>Abies amabilis</i>	Lower	~1.00	21	0.54	1.548±0.056	1.547±0.065	0.278	1.461

Note: Variables measured are described in text: height, qualitative canopy position; branch overlap, number of internodes per observable foliage intercept; mean angle, arithmetic mean of measured internode angles; X' , parameter of the rotated ellipsoidal angle distribution function defined by eq. 2; ITAR, interceptable to total area ratio (values are mean \pm SD); L/W , ratio of internode length to width (values are mean \pm SD); H/W , ratio of internode height to width; K_i , extinction coefficient, estimated for a given species and canopy layer on the basis of the preceding morphological parameters. Values in parentheses are interpolated; branch overlap values for subcanopy *Taxus brevifolia* and *Abies amabilis* are assumed = 1.0.

where θ is the angle from the horizontal, $g(\theta)$ is the probability distribution of θ , and χ is the ratio of the horizontal semiaxis length to the vertical semiaxis length of a spheroid (an ellipsoid with two semiaxis lengths equal).

For $\chi < 1$:

$$[2a] \quad \Lambda = \frac{\chi + (\sin^{-1} \epsilon)}{\epsilon}, \quad \epsilon = (1 - \chi^2)^{1/2}$$

and for $\chi > 1$:

$$[2b] \quad \Lambda = \chi + \frac{\ln[(1 + \epsilon)/(1 - \epsilon)]}{2\epsilon\chi}, \quad \epsilon = (1 - \chi^{-2})^{1/2}$$

Expressions for K_i involving non-flat elements necessarily produce ratios of random variables, mitigating against an analytical solution. We therefore employed a Monte-Carlo simulation procedure to approximate values of K_i for a given species and canopy layer, making the following assumptions.

- (1) Branchlet angles were assumed to be distributed as a rotated ellipsoidal distribution, defined by eq. 2 above (however, note that the angular distribution for individual needles need not follow eq. 2)
- (2) For the purposes of estimating projected area potentially intercepted by vertical line transects, branchlets were approximated as ellipsoidal volumes. The major axis length was considered equal to half of internode length L ($a_1 = 0.5L$), and minor axes with length equal to half of branchlet width W ($a_2 = 0.5W$), and half of branchlet height H ($a_3 = 0.5H$). We also assumed that branchlets were inclined only along the major axis (i.e., were inclined along the main growing axis). The projected area of such an ellipsoid inclined at angle θ onto a horizontal plane was calculated as $A = pa_2a_1 \cos \theta + a_3 \sin \theta$.
- (3) The ratio of branchlet length to width (L/W) was assumed to be lognormally distributed.
- (4) Branchlets were assumed to have a lognormally distributed values for interceptable to total leaf area ratio (ITAR).
- (5) The ratio of branchlet height to width (H/D) was assumed constant.

- (6) For a given species and canopy layer, χ , L/W , H/W , and ITAR were assumed to be independent. Empirical estimates for χ , H/W , and the mean and standard deviation of $\log(L/W)$, and $\log(\text{ITAR})$ were used to calculate K_i for each species and canopy layer. Note that K_i values for conifer species are based on branchlet units for which the projected area may be greater than the total leaf area and may thus take values greater than one. Monte-Carlo simulations were implemented with a C++ program, incorporating numerical approximations of cumulative distribution functions for the lognormal and rotated ellipsoidal distribution functions. The extinction coefficient for each species and canopy layer was estimated using 5000 Monte-Carlo simulations. The final estimate of LAI for a given species and canopy layer was calculated by eq. 1.

Statistical analyses

Statistical analyses were performed using DataDesk version 4.2 (Data Descriptions Inc., Ithaca, N.Y.), and Statistica version 4.1 (Statsoft Inc., Tulsa, Okla.). Deviations of morphological variables from normal or log-normal distributions were tested using Lilliefors' test (Lilliefors 1967). Standard correlation and regression analyses were used to test for statistical independence of morphological variables. Confidence intervals for leaf area index values are based on a normal approximation for the distribution of leaf area per vertical transect sample. Confidence intervals for LAI do not incorporate uncertainty in estimates of morphological characteristics.

Results

Foliage morphology and tests of assumptions

Estimation of LAI on the basis of branchlet intercept data depends on the angular distribution of foliage elements, on foliage geometry (branchlet L/W ratio and H/W ratio), and on the ratio of the interceptable to total leaf area (ITAR) of branchlets. Empirical estimates for these variables are listed in Tables 1 and 2. Typical K_i values for canopy foliage ranged from 0.45 to 0.95. However, in a number of cases

Table 2. Morphological characteristics for dominant understory shrubs and herbs at the Wind River Canopy Crane site.

Species	Mean angle ($^{\circ}$)	X'	K_i
<i>Acer circinatum</i>	11	0.250	0.973
<i>Berberis nervosa</i>	24	0.643	0.873
<i>Gaultheria shallon</i>	31	0.864	0.822
<i>Achlys triphylla</i>	14	0.336	0.953
Other species	23	0.596	0.891

Note: The mean angle is the arithmetic mean of measured internode angles; X' is the parameter of the rotated ellipsoidal angle distribution function; and K_i is the corresponding extinction coefficient.

Table 3. Effects of alternative assumptions of branchlet geometry on stand-level estimates of canopy (trees >5 cm DBH) and total (canopy + understory) LAI.

Geometry	Total LAI	% difference	Canopy LAI	% difference
Ellipsoidal (used)	8.61		6.91	
Spheroidal	8.29	3.7	6.61	4.4
Cylindric	8.00	7.0	6.32	8.6
Flat elliptical	8.70	-1.1	7.01	-1.4
Cubic	7.86	8.7	6.19	10.5

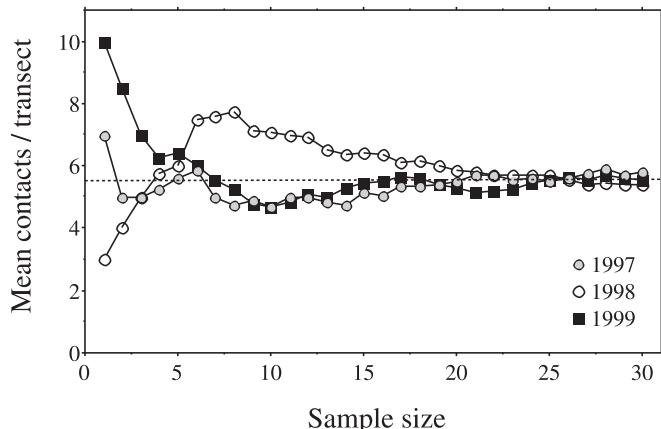
Note: Alternative geometries are compared with the ellipsoidal assumption, judged to be the best geometric approximation and used in subsequent calculations.

species with relatively sparse foliage had estimated K_i values greater than one. The assumptions used in estimating K_i were in close agreement with empirically observed patterns.

- (1) In a separate paper we show that branchlet and leaf angles were approximately distributed as a rotated ellipsoidal distribution, as defined by eq. 2 above (Thomas and Winner 2000).
- (2) The ratio of branchlet length to width (L/W) did not significantly deviate from a lognormal distribution for dominant conifer species at the site (Lilliefors test: $P > 0.50$ for *T. heterophylla* and *P. menziesii*).
- (3) ITAR was likewise approximated by a lognormal distribution (Lilliefors test: $P > 0.50$ for *T. heterophylla* and *P. menziesii*).
- (4) For a given species and canopy layer, branchlet angle, length, width, and ITAR were only very weakly correlated in those few cases where correlations were significant (pairwise r^2 values for the dominant tree species ranged from -0.087 to 0.048).

Two related assumptions used in the calculations are not easily testable: namely, branchlet geometry was approximated as an ellipsoid volume, and the relative thickness of branchlets (H/W ratio) was considered a constant. In both cases, alternative assumptions did not result in large effects on the final results. Plausible alternative assumptions for branchlet geometry are cylindrical and spheroidal volumes. These alternative assumptions were tested using the Monte-Carlo simulation procedure for estimating K_i . In addition, we examined the effect of two relatively implausible geometrical assumptions: that all branchlets were completely flat and that branchlets displayed a cubic geometry. Stand-level esti-

Fig. 1. Mean contact frequency per vertical transect as a function of the number of transects sampled, based on three sets of 30 random points at the Wind River Canopy Crane site, conducted in September 1997, July 1998, and September 1999. All foliage contacts, regardless of plant species, are included.



mates for canopy and total LAI incorporating these assumptions are listed in Table 3. Estimates for total LAI using alternative geometric assumptions were within ~10% in all cases, including the extreme cases of cuboidal and flat foliage displays.

LAI estimates

The average number of observed contacts with foliage layers was 5.8 in 1997, 5.4 in 1998, and 5.7 in 1999. Additional sampling beyond 20 transects yielded relatively little change (<4%) in the average value in any sampling round (Fig. 1). Qualitatively scored uncertainty in intercept counts was low; in only 2 of 90 cases was the vertical line completely obscured from viewing locations above and below the canopy, and in both cases only ~2–3 m of the transect was affected. Of a total of 505 contacts scored, 19 (3.7%) were considered “uncertain.” Following the precedent of optical methods in forest mensuration (such as relascope estimation of basal area: Husch et al. 1982), borderline cases were scored as half of an intercept count.

Whole-stand LAI for the pooled data was estimated as 8.6 ± 1.1 (values listed $\pm 95\%$ confidence interval), of which 1.7 (20%) was understory vegetation, including tall shrubs and trees <5 cm in diameter at breast height (DBH) (Table 3). LAI estimates by year were 9.3 ± 2.1 in 1997, 8.5 ± 2.2 in 1998, and 8.2 ± 1.8 in 1999. In terms of total contribution by species, *T. heterophylla* was dominant, with 3.46 (40% of total LAI), followed by *P. menziesii*, with 2.44 (28%), and *T. plicata*, with 1.27 (15%) (Table 4). Among understory species, *A. circinatum*, *A. triphylla*, *B. nervosa*, *G. shallon*, and *T. brevifolia* each contributed >0.1 unit of LAI (Table 4). Using conventional corrections (Gholz et al. 1976) to convert from projected to total leaf area, HTLAI for the stand is estimated at 9.9 ± 1.4 .

Heterogeneity in canopy structure

Local LAI showed significant variation according to the uppermost species encountered in each vertical transect sample (Fig. 2). Total LAI was highest in samples with

Table 4. Contact frequencies and estimated LAI values for canopy and understory species at the Wind River Canopy Crane site, with data combined among years.

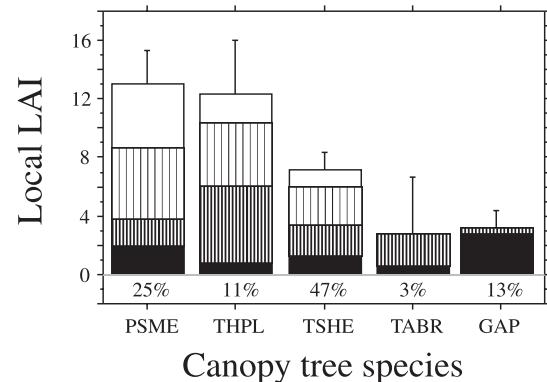
Species	Canopy layer	N_i^*	LAI
<i>Pseudotsuga menziesii</i> [†]	Upper	0.52	1.10
	Middle	0.58	1.11
	Lower	0.12	0.19
<i>Tsuga heterophylla</i> [†]	Upper	0.36	0.57
	Middle	1.27	1.25
	Lower	1.24	1.35
<i>Thuja plicata</i>	Upper	0.12	0.24
	Middle	0.25	0.50
	Lower	0.23	0.47
<i>Taxus brevifolia</i> [†]	Lower	0.16	0.10
<i>Abies amabilis</i> [†]	Lower	0.03	0.02
<i>Acer circinatum</i>	Understory	0.37	0.38
<i>Tsuga heterophylla</i> [†]	Understory	0.23	0.26
<i>Berberis nervosa</i>	Understory	0.18	0.20
<i>Gaultheria shallon</i>	Understory	0.12	0.15
<i>Achlys triphylla</i>	Understory	0.11	0.12
<i>Taxus brevifolia</i> [†]	Understory	0.08	0.08
<i>Abies amabilis</i> [†]	Understory	0.08	0.07
<i>Vaccinium parvifolium</i>	Understory	0.03	0.06
<i>Heuchera</i> sp.	Understory	0.08	0.05
<i>Blechnum spicant</i>	Understory	0.04	0.05
<i>Corylus cornuta</i>	Understory	0.03	0.04
<i>Pteridium aquilinum</i>	Understory	0.03	0.04
<i>Thuja plicata</i>	Understory	0.03	0.04
<i>Athyrium filix-femina</i>	Understory	0.02	0.02
<i>Clintonia uniflora</i>	Understory	0.02	0.02
<i>Polystichum munitum</i>	Understory	0.02	0.02
<i>Vancouveria hexandra</i>	Understory	0.02	0.02
<i>Vaccinium ovalifolium</i>	Understory	0.02	0.02
<i>Actaea rubra</i>	Understory	0.01	0.01
<i>Linnea borealis</i>	Understory	0.01	0.01
<i>Trillium ovale</i>	Understory	0.01	0.01
<i>Viola sempervirens</i>	Understory	0.01	0.01
<i>Xerophyllum tenax</i>	Understory	0.01	0.01
Middle and upper canopy		3.11	4.78
Lower canopy		1.78	2.14
Understory		1.59	1.69
Total		6.48	8.61

* N_i is the branchlet or leaf contact frequency.

[†]For needle-leaved species, N_i is adjusted by a correction factor to account for branchlet overlap within a given horizontal foliage layer.

P. menziesii or *T. plicata* dominant, and lower in samples dominated by *T. heterophylla* or in gaps (indicated by transects with no foliage contacts in the upper or midcanopy layers) (ANOVA, $F = 14.27$, $P < 0.001$). Samples with *T. heterophylla* or *T. plicata* dominant had understory LAI values averaging 1.4 and 0.9, respectively, while gap samples had understory LAI values of ~3.0 (ANOVA, $F = 4.89$, $P = 0.013$). Transects with *P. menziesii* dominant were intermediate, with an average understory LAI of ~2.1. The number of understory species encountered in each transect showed a similar trend (though not statistically significant), with approximately one understory species per transect in gap and *P. menziesii* sites, but values of 0.8 and 0.4 under *T. heterophylla* and *T. plicata*, respectively.

Fig. 2. Local LAI as a function of the uppermost tree species encountered, estimated on the basis of pooled vertical line intercept data at the Wind River Canopy Crane site (PSME, *Pseudotsuga menziesii*; THPL, *Thuja plicata*; TSHE, *Tsuga canadensis*; TABR, *Taxus brevifolia*; GAP, no mid- or upper-canopy foliage encountered). Shading corresponds to canopy layer, arranged from bottom to top as understory, lower-canopy, mid-canopy, and upper-canopy foliage. The proportions of sample points within each category are listed below each bar.



Discussion

Estimation of LAI using the line-intercept method described was found to be logically tractable and repeatable, given canopy access as provided by the crane facility at the study site. The first important logistical issue to address was that of visibility: we had initially anticipated that randomly placed vertical lines might commonly be obscured in dense foliage, making it impossible to obtain accurate counts. However, in practice this difficulty was encountered in <3% (2/90) of the random line drops. The second logistical issue was that of difficulty in maintaining a still, vertically positioned line under field conditions. Intercept counts qualitatively scored as uncertain as a consequence of these problems accounted for less than 4% of the total intercept counts. Repeated use of the method also yielded consistent overall LAI values, with estimates equal to 9.3, 8.5, and 8.2 over the 3 years. Several large Douglas-firs and other dominant trees within the crane circle died during the course of the study. The temporal decline in LAI, although not statistically significant, may thus possibly represent more than a stochastic sampling effect.

The LAI values presented are necessarily based on assumptions and simplifications, violations of which could potentially introduce bias. Analyses of morphological data indicated that assumptions concerning leaf angle distributions and branchlet geometry were reasonable approximations. Branchlet geometry was approximated as an ellipsoidal volume. Although this assumption is difficult to test directly, modification of the Monte-Carlo simulation program to incorporate other reasonable geometric approximations of branchlet shape suggests that this assumption did not have a very large effect on the overall LAI estimate. In addition, because not all parts of the canopy were accessible by the canopy crane, it was not possible to conduct a formal randomization for measurements of branchlet morphology.

The estimates of K_t therefore rely on collection of "representative" samples of accessible foliage. Thus, an additional possible source of bias is a systematic difference in branchlet morphology between outer, accessible parts of tree crowns, and inner parts of the crown close to the trunk. As with most tree species, foliage in old-growth Douglas-fir and western hemlock is heavily concentrated in the most exposed portions of the crown. We therefore reason that any bias related to oversampling relatively exposed foliage is also likely to be small.

Leaf area index values vary spatially and temporally within all ecosystems, including those dominated by trees with "evergreen" phenology (e.g., Penner and Deblonde 1996; Chen 1996). In the present study the spatial scale is the radius of the canopy crane circle, and we explicitly randomly sampled within this area. There may also be substantial year-to-year variation in leaf area index, resulting from variation in climate, phenology, and successional changes in species composition, among other factors. In particular, leaf losses due to winter storm damage are likely to vary greatly among years. For example, a February 1997 ice storm resulted in a loss of ~1.5 LAI from canopy trees at the study site (based on visual approximations of foliage material on snow following the storm: S.C. Thomas and W.E. Winner, personal observations). On this basis alone, one might expect LAI at the site to vary from between ~7 and 10 from year to year.

There has been considerable recent interest in comparing "ground truth" estimates of forest LAI to remote sensing data (e.g., Spanner et al. 1994; White et al. 1997; Lefsky et al. 1999). Allometric estimates based on sapwood area or DBH have commonly been used for this purpose. However, there is evidence for both differences in sapwood-LAI relationships among species (Snell and Brown 1978; Kaufmann and Troendle 1981; Waring et al. 1982), and for site-to-site differences within individual species (Berninger and Nikinmaa 1994; Callaway et al. 1994). Similarly, LAI estimates based on inversion of gap fraction or light penetration data must be adjusted for differences in foliage aggregation, a factor that shows large differences among species and among sites (e.g., Gower and Norman 1991; Smith et al. 1993; Kühner and Mosandl 2000), and which varies seasonally (Chen 1996). The vertical line-intercept method developed here expands the range of methods available for measuring LAI in coniferous forests. Estimates of LAI in which all parameters are measured on-site should ultimately provide a sound basis for calibrating other, less direct but more rapid methods for LAI estimation in evergreen forest stands.

LAI values of ~8.6 in old-growth Douglas-fir stands are similar to those reported from a variety of other forest ecosystems. LAI values for warm-temperate evergreen forests in Japan fell in the range of 7.4–8.8 (Kira et al. 1969), and destructive samples in a tropical rain forest in Malaysia yielded an estimate of ~8.0 (Kato et al. 1978). More recently, relatively high values have been reported in some temperate deciduous forests, including values up to 8.4 in stands of *Acer saccharum* Marsh. (Fassnacht and Gower 1997) and 9.1 in *Castanea sativa* Mill. (Tokar 1997). Recent estimates for conifers include estimates of up to ~10 in *Picea abies* (L.) Karst. stands in Poland (Kram 1998) and 10.8 in *Pinus ponderosa* Dougl. ex Laws. in Montana (O'Hara 1996).

To the degree that spatial variability within the stand corresponds to temporal patterns, the data presented may also give an indication of changes in LAI through succession in Douglas-fir stands. Local LAI values of ~13 were found in vertical transects in which Douglas-fir trees were the dominant species, compared with values of ~7 in western hemlock dominated locations. These values likely bracket the range of LAI occurring in Douglas-fir – western hemlock ecosystems. The local differences further suggest that the highest LAI values may obtain in younger stands where the upper canopy is completely dominated by Douglas-fir and that LAI generally declines as hemlock replaces Douglas-fir in very old stands.

Acknowledgments

We thank the staff of the Wind River Canopy Crane, Mark Creighton, Andrew Baker, and Dave Shaw, for their assistance with field measurements and David Ford, Tom Hinckley, and Doug Sprugel for helpful input at various stages of the project. Clifton Cooper and Sarah McCarthy are also thanked for assistance with canopy sampling and morphological measurements. This work was supported by a grant from the National Institute for Global Environmental Change (NIGEC-WESTGEC).

References

- Alexandre, D.Y. 1981. L'indice foliaire des forêts tropicales. *Acta Oecol. Oecol. Gen.* **2**: 299–312.
- Anderson, M.C. 1966. Stand structure and light penetration. II. A theoretical analysis. *J. Appl. Ecol.* **3**: 41–54.
- Barclay, H.J., and Goodman, D. 2000. Conversion of total to projected leaf area index in conifers. *Can. J. Bot.* **78**: 447–454.
- Berninger, F., and Nikinmaa, E. 1994. Foliage area – sapwood area relationships of Scots pine (*Pinus sylvestris*) trees in different climates. *Can. J. For. Res.* **24**: 2263–2268.
- Callaway, R.M., DeLucia, E.H., and Schlesinger, W.H. 1994. Biomass allocation of montane and desert ponderosa pine—an analog of response to climate change. *Ecology*, **75**: 1474–1481.
- Campbell, G.S. 1986. Extinction coefficients for radiation in plant canopies calculated using an ellipsoidal inclination angle distribution. *Agric. For. Meteorol.* **36**: 317–321.
- Campbell, G.S. 1990. Derivation of an angle density function for canopies with ellipsoidal leaf angle distributions. *Agric. For. Meteorol.* **49**: 3173–176.
- Campbell, G.S., and Norman, J.M. 1989. The description and measurement of plant canopy structure. In *Plant canopies: their growth, form and function*. Edited by G. Russell, B. Marshall, and P.G. Jarvis. Cambridge University Press, Cambridge, U.K. pp. 1–19.
- Chen, J.M. 1996. Optically-based methods for measuring seasonal variation in leaf area index in boreal conifer stands. *Agric. For. Meteorol.* **80**: 135–163.
- Chen, J.M., and Black, T.A. 1992. Defining leaf area index for non-flat leaves. *Agric. For. Meteorol.* **57**: 1–12.
- Chen, J.M., and Cihlar, J. 1995. Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. *IEEE Trans. Geosci. Remote Sens.* **33**: 777–787.

- Chen, J.M., and Cihlar, J. 1996. Retrieving leaf area index of boreal conifer forests using LANDSAT TM images. *Remote Sens. Environ.* **55**: 153–162.
- Cutini, A., Matteucci, G., and Mugnozza, G.S. 1998. Estimation of leaf area index with the LI-COR LAI 2000 in deciduous forests. *For. Ecol. Manage.* **105**: 55–65.
- DeBell, D.S., and Franklin, J.F. 1987. Old-growth Douglas-fir and western hemlock: a 36-year record of growth and mortality. *West. J. Appl. For.* **2**: 111–114.
- DeBlonde, G., Penner, M., and Royer, A. 1994. Measuring leaf area index with the LI-COR LAI-2000 in pine stands. *Ecology*, **75**: 1507–1511.
- Diggle, P.J. 1983. Statistical analysis of spatial point patterns. Academic Press, London.
- Fassnacht, K.S., Gower, S.T., Norman, J.M., and McMurtrie, R.E. 1994. A comparison of optical and direct methods for estimating foliage surface area index in forests. *Agric. For. Meteorol.* **71**: 183–207.
- Ford, E.D., and Newbould, P.J. 1971. The leaf canopy of a coppiced deciduous woodland. I. Development and structure. *J. Ecol.* **59**: 843–862.
- Franklin, J.F., and Waring, R.H. 1981. Distinctive features of the northwestern coniferous forest: development, structure, and function. In *Forests: fresh perspectives from ecosystem analysis*. Edited by R.H. Waring. Oregon State University Press, Corvallis. pp. 59–86.
- Franklin, J.F., Hall, F.C., Dyrness, C.T., and Maser, C. 1972. Federal research natural areas in Oregon and Washington: a guidebook for scientists and educators. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oreg.
- Franklin, S.E., Lavigne, M.B., Deuling, M.J., Wulder, M.A., and Hunt, E.R. 1997. Estimation of forest leaf area index using remote sensing and GIS data for modelling net primary production. *Int. J. Remote Sens.* **18**: 3459–3471.
- Fassnacht, K.S., and Gower, S.T. 1997. Interrelationships among the edaphic and stand characteristics, leaf area index, and above-ground net primary production of upland forest ecosystems in north central Wisconsin. *Can. J. For. Res.* **27**: 1058–1067.
- Gholz, H.L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology*, **63**: 469–481.
- Gholz, H.L., Fitz, F.K., and Waring, R.H. 1976. Leaf area differences associated with old-growth forest communities in the western Oregon Cascades. *Can. J. For. Res.* **6**: 49–57.
- Gower, S.T., and Norman, J.M. 1991. Rapid estimation of leaf area index in conifer and broad-leaf plantations. *Ecology*, **72**: 1896–1900.
- Grier, C.C., and Running, S.W. 1977. Leaf area of mature northwestern coniferous forests: relation to water balance. *Ecology*, **58**: 893–899.
- Groeneveld, D.P. 1997. Vertical point quadrat sampling and an extinction factor to calculate leaf area index. *J. Arid Environ.* **36**: 475–485.
- Hitchcock, C.L., and Cronquist, A. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.
- Husch, B., Miller, C.I., and Beers, T.W. 1982. Forest mensuration. John Wiley & Sons, New York.
- Ishii, H., Reynolds, J.H., Ford, E.D., and Shaw, D.C. 2000. Height growth and vertical development of an old-growth *Pseudotsuga-Tsuga* forest in southwestern Washington State, U.S.A. *Can. J. For. Res.* **30**: 17–24.
- Jack, S.B., and Long, J.N. 1991. Response of leaf area index to density for two contrasting tree species. *Can. J. For. Res.* **21**: 1760–1764.
- Jarvis, P.G., and Leverenz, J.W. 1983. Productivity of temperate, deciduous and evergreen forests. In *Physiological plant ecology: new series*. Edited by O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler. Springer-Verlag, New York. pp. 233–280.
- Kato, R., Tadaki, Y., and Ogawa, H. 1978. Plant biomass and growth increment studies in Pasoh Forest. *Malay. Nat. J.* **30**: 211–224.
- Kaufmann, M.R., and Troendle, C.A. 1981. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. *For. Sci.* **27**: 477–482.
- Kimball, J.S., Thornton, P.E., White, M.A., and Running, S.W. 1997. Simulating forest productivity and surface-atmosphere carbon exchange in the BOREAS study region. *Tree Physiol.* **17**: 589–599.
- Kira, T. 1978. Community architecture and organic matter dynamics in tropical lowland rainforests of Southeast Asia with special reference to Pasoh Forest, West Malaysia. In *Tropical trees as living systems*. Edited by P.B. Tomlinson and M.H. Zimmermann. Cambridge University Press, Cambridge, U.K. pp. 561–90.
- Kira, T., Shinozaki, K., and Hosumi, K. 1969. Structure of forest canopies as related to their primary productivity. *Plant Cell Physiol.* **10**: 129–142.
- Kram, K.J. 1998. Influence of species composition and forest age on leaf area index. *Pol. J. Ecol.* **46**: 75–88.
- Küßner, R., and Mosandl, R. 2000. Comparison of direct and indirect estimation of leaf area index in mature Norway spruce stands of eastern Germany. *Can. J. For. Res.* **30**: 440–447.
- Lefsky, M.A., Cohen, W.B., Acker, S.A., Parker, G.G., Spies, T.A., and Harding, D. 1999. Lidar remote sensing of the canopy structure and biophysical properties of Douglas-fir western hemlock forests. *Remote Sens. Environ.* **70**: 339–361.
- Lilliefors, H.W. 1967. On the Kolmogorov-Smirnov test for normality with mean and variance unknown. *J. Am. Stat. Assoc.* **64**: 399–402.
- Marshall, J.D., and Waring, R.H. 1986. Comparison of methods of estimating leaf-area index in old-growth Douglas-fir. *Ecology*, **67**: 975–979.
- Martens, S.N., Ustin, S.L., and Rousseau, R.A. 1993. Estimation of tree canopy leaf area index by gap fraction analysis. *For. Ecol. Manage.* **61**: 91–108.
- Nemani, R.R., and Running, S.W. 1989. Testing a theoretical climate – soil – leaf area hydrologic equilibrium of forests using satellite data and ecosystem simulation. *Agric. For. Meteorol.* **44**: 245–260.
- O'Hara, K.L. 1996. Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. *For. Sci.* **42**(33): 1–34.
- Parker, G.G. 1995. Structure and microclimate of forest canopies. In *Forest canopies*. Edited by M.D. Lowman and N.M. Nadkarni. Academic Press, New York. pp. 73–106.
- Parker, G.G. 1997. Canopy structure and light environment of an old-growth Douglas-fir/western hemlock forest. *Northwest Sci.* **71**: 261–270.
- Parker, G.G., O'Neil, J.P., and Higman, D. 1989. Vertical profile and canopy organization in a mixed deciduous forest. *Vegetatio*, **89**: 1–12.
- Penner, M., and DeBlonde, G. 1996. The relationship between leaf area and basal area growth in jack and red pine trees. *For. Chron.* **72**: 170–175.
- Potter, C.S., Randerson, J.T., Field, C.B., Matson, P.A., Vitousek, P.M., Mooney, H.A., and Klooster, S.A. 1993. Terrestrial eco-

- system production—a process model based on global satellite and surface data. *Global Biogeochem. Cycles*, **7**: 811–841.
- Sampson, D.A., and Allen, H.L. 1995. Direct and indirect estimates of leaf area index (LAI) for lodgepole and loblolly pine stands. *Trees*, **9**: 226–237.
- Smith, N.J., Chen, J.M., and Black, T.A. 1993. Effects of clumping on stand leaf area index using the LI-COR LAI-2000. *Can. J. For. Res.* **23**: 1940–1943.
- Snell, J.A., and Brown, J.K. 1978. Comparison of tree biomass estimators—DBH and sapwood area. *For. Sci.* **24**: 455–457.
- Spanner, M.A., Johnson, L., Miller, J., McCreight, R., Freemantle, J., Runyon, J., and Gong, P. 1994. Remote sensing of seasonal leaf area index across the Oregon transect. *Ecol. Appl.* **4**: 258–271.
- Stenberg, P., DeLucia, E.H., Schoettle, A.W., and Smolander, H. 1995. Photosynthetic light capture and processing from cell to canopy. In *Resource physiology of conifers*. Edited by W.K. Smith and T.M. Hinckley. Academic Press, New York. pp. 3–38.
- Thomas, S.C., and Bazzaz, F.A. 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. *Ecology*, **80**: 1607–1622.
- Thomas, S.C., and Ickes, K. 1995. Ontogenetic changes in leaf size in Malaysian rain forest trees. *Biotropica*, **27**: 427–434.
- Thomas, S.C., and Winner, W.E. 2000. A rotated ellipsoidal angle density function improves estimation of foliage inclination distributions in forest canopies. *Agric. For. Meteorol.* **100**: 19–24.
- Tokar, F. 1997. Aboveground dendromass formation in relation to the leaf area index of mixed forest stands of Spanish chestnut (*Castanea sativa* Mill). *Ekologia (Bratislava)*, **16**: 23–31.
- Turner, D.P., Acker, S.A., Means, J.E., and Garman, S.L. 2000. Assessing alternative allometric algorithms for estimating leaf area of Douglas-fir trees and stands. *For. Ecol. Manage.* **126**: 61–76.
- Van Gardingen, P.R., Jackson, G.E., Hernandez-Daumas, S., Russell, G., and Sharp, L. 1999. Leaf area index estimates obtained for clumped canopies using hemispherical photography. *Agric. For. Meteorol.* **94**: 243–257.
- Van Pelt, R., and North, M.P. 1996. Analyzing canopy structure in Pacific Northwest old-growth forests with a stand-scale crown model. *Northwest Sci.* **70**(Spec. Issue): 15–30.
- Waring, R.H., Emmingham, W.H., Ghosh, H.L., and Grier, C.C. 1978. Variation in maximum leaf area of coniferous forests in Oregon and its ecological significance. *For. Sci.* **24**: 131–140.
- Waring, R.H., Schroeder, P.E., and Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. *Can. J. For. Res.* **12**: 556–560.
- Warren-Wilson, J. 1963. Errors resulting from thickness of point quadrats. *Aust. J. Bot.* **11**: 178–188.
- Warren-Wilson, J. 1965. Stand structure and light penetration. I. Analysis by point quadrats. *J. Appl. Ecol.* **2**: 383–390.
- Watson, D.J. 1947. Comparative physiological studies in the growth of field crops: I: Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Ann. Bot. (London)*, **11**: 41–76.
- Westman, W.E., and Whittaker, R.H. 1975. The pygmy forest region of northern California: studies on biomass and primary productivity. *J. Ecol.* **63**: 493–520.
- White, J.D., Running, S.W., Nemani, R., Keane, R.E., and Ryan, K.C. 1997. Measurement and remote sensing of LAI in Rocky Mountain montane ecosystems. *Can. J. For. Res.* **27**: 1714–1727.
- Whittaker, R.H., and Woodwell, G.M. 1968. Surface area relations of woody plants and forest communities. *Am. J. Bot.* **54**: 931–939.
- Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., and Kaufman, M.R. 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* **40**: 513–527.