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Assessing alternative allometric algorithms for estimating leaf area of Douglas-fir trees and stands

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Abstract

Allometric approaches based only on tree diameter at breast height (DBH) have been used to estimate leaf biomass and leaf area index (LAI) in coniferous forests. This approach has been suggested to sometimes produce unrealistically high LAI estimates, notably in old-growth stands in the Pacific Northwest (PNW). Leaf area to sapwood area relationships offer an alternative basis for estimating LAI and a number of empirical and modeling approaches have been used for generating tree-level sapwood area and leaf area estimates. To evaluate effects of the alternative assumptions among these approaches, we compared five algorithms for estimating leaf area per tree and stand-level LAI in stands dominated by Douglas-fir (*Pseudotsuga menziesii* var *menziesii*). Initially, 383 trees representing the major species and the complete range of tree sizes in the study area were examined for species, DBH, crown ratio, and sapwood area. There were significant species-specific relationships between sapwood and DBH for these trees. Neither crown ratio nor the ratio of observed tree height to expected tree height were effective in predicting the sign and magnitude of the residuals in the sapwood area/DBH relationships. Nine stands (three young, three mature, and three old-growth) in and near the H.J. Andrews Experimental Forest in the western central Oregon Cascades were then studied with species, DBH, and crown ratio recorded for all trees in a set of subplots. At the stand level, the LAI algorithms based on sapwood area at breast height produced significantly lower LAI estimates than the DBH-alone algorithm in mature and old-growth stands. The algorithm relying on estimated sapwood area at the base of the crown further reduced LAI estimates relative to those based on sapwood area at breast height. Although the differences between the DBH-based and sapwood area-based approaches tended to be greatest in the older stands, estimated LAI was higher in the older stands than in the younger stands for all algorithms. Comparative studies using allometric, litterfall, and optical approaches to LAI estimation are needed to resolve issues such as trends in LAI with succession and maximum possible LAI in Douglas-fir forests. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Douglas-fir; Leaf area index; Sapwood area; Sapwood width; Crown ratio; Old growth

1. Introduction

The foliage surface area of a forest strongly influences light and water interception, and hence rates of photosynthesis, evaporation, and transpiration (War-

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ing, 1983; Vose and Swank, 1990). The leaf area index (LAI) of a stand, i.e., projected leaf area per unit surface area of the ground, is thus used as an input to several process-based forest productivity and hydrology models (Woodward, 1987; Neilson, 1995; Ryan et al., 1996). These models are increasingly being applied in a spatially-distributed mode for the purposes of characterizing spatial patterns in productivity and potential responses to climatic change (Neilson and Marks, 1994; Wigmosta et al., 1994; Milner et al., 1996; VEMAP Participants, 1995). LAI is also estimated for simulating biosphere–atmosphere interactions in general circulation models of the atmosphere (Bonan, 1995; Chase et al., 1996). The need for LAI estimates at landscape to global scales in these modeling efforts has prompted extensive research on measurement of LAI at the plot level and the application of satellite remote sensing for generating geographic data layers for LAI (Peterson and Running, 1989; Baret, 1995; Myneni et al., 1997; White et al., 1997; Turner et al., in press).

The development of algorithms relating spectral vegetation indices (SVIs) from satellite imagery to LAI relies on the accurate measurement of LAI at georeferenced sites over the range of potential LAI values (e.g. Spanner et al., 1994). However, measurement of this important parameter in mature to old-growth conifer forest stands is problematical whether based on litterfall, interception of light, or allometry. LAI estimates based on measured litterfall, specific leaf area, and needle retention time assume that foliar biomass is in steady state and may require several years to accommodate interannual variability (Trofymow et al., 1991). Estimates based on light interception can be compromised by the heterogeneity of the canopy, have poor discriminating power for high values of LAI, and in any case should be calibrated or validated with more direct methods (Smith et al., 1991; Fassnacht et al., 1994; Gower et al., in press). Allometric approaches based only on diameter at breast height (DBH) appear to yield unrealistically high LAI estimates (Marshall and Waring, 1986). Besides affecting the development of LAI–SVI relationships, the limitations in the various methodologies have introduced considerable uncertainty regarding the maximum LAI which can be attained in these forests and about trends in LAI during succession.

In addition to the commonly used allometric approach based on tree DBH, alternative approaches to estimating LAI based on measurement or estimation of sapwood cross-sectional area have been employed (Maguire and Batista, 1996). Measurements of sapwood area and foliar biomass (or leaf area) using destructive harvests have found in many cases nearly linear relationships between the two variables, with the leaf area (A_l) supported per unit of sapwood area (A_s) varying by species (Grier and Waring, 1974; Kaufmann and Troendle, 1981; Waring et al., 1982; Margolis et al., 1995; O'Hara and Valappil, 1995). The physiological basis for the relationship lies in the observations that water transport in trees occurs almost exclusively in the sapwood (Kramer and Kozlowski, 1979), that species differ in the saturated permeability of their sapwood (Whitehead et al., 1984), and that experimental reductions in leaf area result in reductions in sapwood area (Margolis et al., 1988). The theoretical basis for the relationships originates from pipe model theory (Shinozaki et al., 1964; Waring et al., 1982). Although some studies have shown intraspecific variation in the ratio of A_l to A_s (Dean and Long, 1986; Bancalari et al., 1987; Thompson, 1989; Mencuccini and Grace, 1995), for the purposes of estimating stand-level leaf area, the assumption is often made that the ratio is a species-specific property (Margolis et al., 1995).

In this study, we applied several variations of the $A_l : A_s$ approach to estimating tree and stand leaf area in young, mature, and old-growth Douglas-fir stands in western Oregon. Results were compared with each other and a purely DBH-based approach to identify effects of alternative sets of assumptions. Relationships of measured DBH to sapwood area and possible interactive effects of crown ratio and tree height were also examined to evaluate possible predictors of sapwood area.

2. Methods

2.1. The study area

The trees and stands examined in this study were located in or near the H.J. Andrews Experimental Forest (HJA) on the west slope of the Cascade Range in Oregon (Van Cleve and Martin, 1991). The climate in this region is characterized by mild, wet winters and warm, dry summers and favors development of temperate coniferous forests (Waring and Franklin, 1979). The mild year-round climate at HJA is associated with relatively high LAIs (Waring et al., 1978; Gholz et al., 1976; Grier and Running, 1977; Gholz, 1982). As a result of timber harvesting, the area is very heterogeneous with respect to stand age, ranging from recent clear-cuts to stands over 500 years of age.

Because some of the LAI algorithms require species-specific information on DBH/height and DBH/sapwood area relationships, a set of trees with representatives from all size classes of the three major species [$n = 221$ for Douglas-fir (*Pseudotsuga menziesii*), $n = 111$ for western hemlock (*Tsuga heterophylla*), and $n = 51$ for western redcedar (*Thuja plicata*)] were initially studied in detail. All trees were located within a set of 26 stands studied by Means et al. (1999). After species and DBH were recorded, height and crown ratio were determined by clinometer and distance measurements, and trees were cored from two directions for measurement of sapwood width to the nearest mm.

For each species, a least-squares regression (see below) was fit to the set of DBH/sapwood area measurements. The residuals in those plots were examined in relation to two indicators of tree vigor. First was the crown ratio and second was the ratio of measured tree height to expected tree height. The expected tree heights were from species-specific DBH/height equations for trees from the Northern Oregon Cascades Garman et al. (1995). The coefficients of determination was used to assess the strength of the relationships.

2.2. Tree-level leaf area algorithms

For the set of 383 trees for which sapwood width was measured, leaf area per tree was estimated in five ways for each tree (Table 1). The first algorithm was based on DBH alone. Other algorithms were alternative formulations based on projected leaf area (A_l) to sapwood cross-sectional area (A_s) relationships.

2.2.1. DBH-based allometric approach (LAI_{DBH})

This approach relied on earlier studies at HJA in which destructive sampling was used to quantitatively relate DBH and foliar biomass (Gholz et al., 1979). The general form of the equation relating these two variables was:

$$\mathrm{FB} = \exp^{(a+(b\times\ln(\mathrm{DBH})))} \qquad (1)$$

where FB is the foliar biomass (kg per tree), a and b the species-specific coefficients (Table 2), and DBH the diameter at breast height.

The DBH range in the original studies generally extended to trees >150 cm (Gholz et al., 1979) near the maximum for trees in this study. Foliar biomass was converted to all-sided and projected leaf area using

Table 1
Summary of algorithms used for estimating tree-level LAI. Parameters for all algorithms are species-specific

LAI_{DBH}	Foliar biomass estimated from DBH, foliar biomass converted to all-sided leaf area with specific leaf area, all-sided leaf area converted to projected leaf area with cross-sectional correction factor
LAI_{sabhm}	Sapwood area at breast height measured by tree coring. Sapwood area converted to projected leaf area with ratio of projected leaf area to sapwood area at breast height
LAI_{sabhr}	Sapwood area at breast height estimated from linear regression of observed DBH to observed sapwood area. Sapwood area converted to projected leaf area with ratio of projected leaf area to sapwood area at breast height
LAI_{sabhz}	Sapwood width at breast height estimated from DBH using the approach in the ZELIG–PNW model, sapwood area at breast height computed from sapwood width and DBH, sapwood area converted to projected leaf area with ratio of projected leaf area to sapwood area at breast height
LAI_{sachz}	Sapwood width at breast height estimated from DBH as in LAI_{sabhz} and assumed to be same at the base of the crown. Diameter inside bark at the base of the crown derived from a taper equation from ZELIG–PNW with inputs of DBH, tree height and crown ratio. Sapwood area at the base of the crown converted to projected leaf area with a ratio, specific to the base of the crown, of projected leaf area to sapwood area

Table 2
Species-specific parameters (see Eq. (1)) for relating DBH to foliar biomass, and foliar biomass to leaf area

Species	Coefficient a [a]	Coefficient b [a]	Specific leaf area [b] ($cm^2\ g^{-1}$)	Cross-sectional correction [b]
Douglas-fir	−2.846	1.701	177	2.36
Western hemlock	−4.130	2.128	189	2.14
Western recedar	−2.617	1.782	176	3.00

[a] Gholz et al., 1979.
[b] Gholz et al., 1976.

specific leaf areas ($cm^2\ g^{-1}$) and cross-sectional correction factors from the literature (Table 2).

2.2.2. Sapwood area at breast height from measured DBH and sapwood width (LAI_{sabhm})

As noted, sapwood width was measured using tree cores. Sapwood cross-sectional area at breast height was then estimated by:

$$A_{\mathrm{sbh}} = (\Pi(\mathrm{DBH}_{\mathrm{ib}}/2)^2) - (\Pi((\mathrm{DBH}_{\mathrm{ib}}/2) - \mathrm{SW})^2) \tag{2}$$

where A_{sbh} is the sapwood area at breast height, $\mathrm{DBH}_{\mathrm{ib}}$ the diameter inside bark defined as DBH(1 − bark width factor (Table 3)), and SW the sapwood width.

A_{sbh} was converted to projected leaf area using species-specific $A_{\mathrm{l}} : A_{\mathrm{sbh}}$ relationships from the literature (Table 3).

2.2.3. Sapwood area at breast height using locally-derived regressions of sapwood area at breast height against DBH (LAI_{sabhr})

An alternative estimate for A_{sbh} was generated for each tree from species-specific relationships (equation form in Table 4) of DBH to sapwood area for the trees cored in this study. The same $A_{\mathrm{l}} : A_{\mathrm{sbh}}$ relationships as in Algorithm 2 were then used for conversion to projected leaf area.

2.2.4. Sapwood area at breast height using the ZELIG–PNW approach (LAI_{sabhz})

ZELIG is a forest succession gap model designed to study trends in stand structure and composition as a function of management and climate (Garman et al., 1992; Urban, 1993; Urban et al., 1993). In the model, sapwood width at breast height is estimated using

Table 3
Species-specific parameters (see Eq. (3)) for relating DBH to sapwood width and projected leaf area (A_{l}) to sapwood area at breast height (A_{sbh}) or sapwood area at the base of the crown (A_{sch})

Species	Coefficient c [a]	Coefficient d [a]	Bark width [b] factor	$A_{\mathrm{l}} : A_{\mathrm{sbh}}$ [c] ($m^2\ cm^{-2}$)	$A_{\mathrm{l}} : A_{\mathrm{sch}}$ [c] ($m^2\ cm^{-2}$)
Douglas-fir	5.43	0.0460	0.11	0.47	0.54
Western hemlock	16.30	0.0178	0.04	0.41	0.46
Western redcedar	4.67	0.0341	0.05	0.50	0.56

[a] Urban, 1993.
[b] Garman, unpublished.
[c] Waring et al., 1982.

Table 4
Species-specific coefficients for DBH–sapwood area relationships

Species	Coefficient e	Coefficient f	N	R^2
Douglas-fir [a]	−96.28	12.60	221	0.80
Western hemlock [b]	6.14	1.26	111	0.85
Western redcedar [a]	−68.09	7.85	51	0.91

[a] Sapwood area (cm^2) = coefficient k + coefficient l × DBH (cm).
[b] Sapwood area (cm^2) = coefficient k + $\mathrm{DBH}^{\mathrm{coefficient\ l}}$.

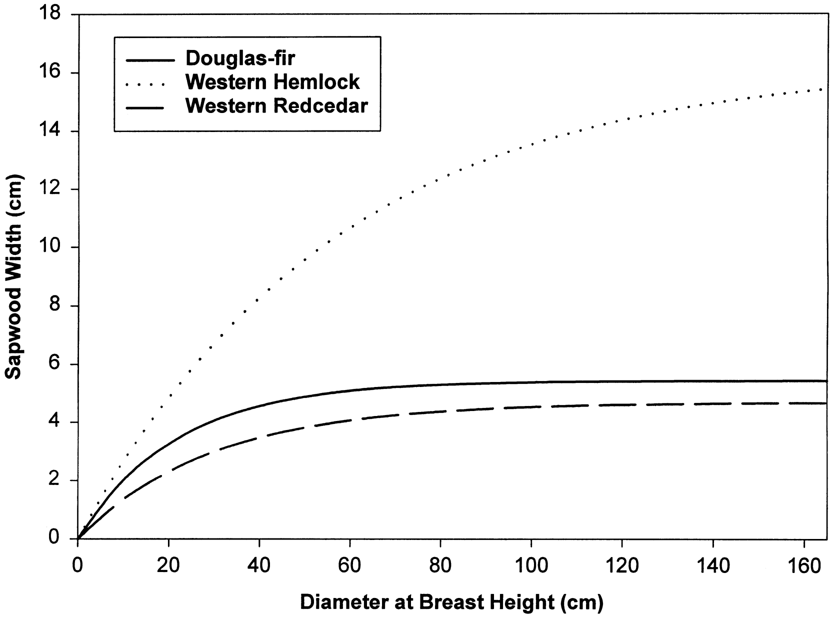

Fig. 1. Species-specific relationships of diameter at breast height to sapwood width (see Eq. (2), Table 3). Equation form from Urban (1993).

species-specific equations of the form:

$$\mathrm{SW} = c(1 - \exp^{(-d\times\mathrm{DBH})}) \quad (3)$$

where SW is the sapwood width (cm), c the coefficient related to maximum sapwood width (Table 3), and d the coefficient related to curve shape (Table 3).

The form of the equation and the c and d coefficients have been determined previously for the major western tree species in association with the development of a Pacific Northwest (PNW) version of ZELIG. The ZELIG–PNW parameterization (Fig. 1) is based on observations of DBH and sapwood width for Douglas-fir and other conifers throughout the region (Wellwood and Jarazs, 1966; Lassen and Okkonen, 1969). For this algorithm, sapwood area at breast height was then converted to leaf area as in the $\mathrm{LAI}_{\mathrm{sabhm}}$ algorithm.

2.2.5. Sapwood area at the base of the crown using the ZELIG–PNW approach (LAI_{sachz})

This formulation for leaf area per tree is the complete algorithm used in the ZELIG–PNW model. The leaf area per tree is based on estimated sapwood area at the base of the crown, which is derived from simulated or measured tree DBH and height to the base of the crown. For this application, height to the base of the crown was determined from measured tree heights and crown ratios. Tree diameter inside bark at the base of the crown ($\mathrm{DCH}_{\mathrm{ib}}$) was estimated from:

$$\mathrm{DCH}_{\mathrm{ib}} = \mathrm{DBH} \times \mathrm{TF} \quad (4)$$

where DBH is the diameter at breast height,

$$\mathrm{TF} = (g - h(\mathrm{HC}/\mathrm{HT}) + i(\mathrm{HC}^2/\mathrm{HT}^2))^{1/2} \quad (5)$$

and TF the taper factor, g, h, and i the species-specific coefficients (Table 5), HC the height at the base of the crown, and HT the height of the tree.

The taper equation is based on the allometric studies of Kozak et al. (1969). The g, h, and i coefficients were derived from the optical dendrometer dataset in the Oregon State University Forest Research Laboratory Databank (Dataset AND001 in Michener et al., 1990). In ZELIG–PNW, sapwood width is assumed to be the same at breast height and at the base of the crown (c.f. Brix and Mitchell, 1983). Sapwood area at the base of the crown (A_{sch}) was estimated using the formulation in Eq. (2) but with $\mathrm{DCH}_{\mathrm{ib}}$. For Douglas-fir, western hemlock and several other species, $A_{\mathrm{l}} : A_{\mathrm{sch}}$ has been determined using destructive sampling (Waring et al., 1982). For western redcedar and other species not previously studied, $A_{\mathrm{l}} : A_{\mathrm{sch}}$ was approximated based

Table 5
Species-specific coefficients (Eq. (4)) for the taper factor (Urban, 1993)

Species	Coefficient g	Coefficient h	Coefficient i	N	R^2
Douglas-fir	0.8720	1.4807	0.6088	216	0.95
Western hemlock	1.1112	1.6953	0.5841	352	0.85
Western redcedar	1.1921	2.3842	1.1921	53	0.92

on $A_l : A_{sch}$ from other species. These ratios (Table 3) were then used to compute projected leaf area.

2.3. Stand-level LAI estimates

Nine stands dominated by Douglas-fir were studied. Stands were classified as young (20–80 years), mature (80–200 years), or old-growth (+200 years) based on stand structure (Spies and Franklin, 1991) and three stands from each age class were represented. Species composition was predominantly Douglas-fir, western hemlock, and western redcedar (>95% of basal area).

In each stand, a 50×50 m^2 plot (with dimensions corrected for slope angle) was laid out. Depending upon the density of canopy trees, trees were then measured in the entire plot, or in five or nine circular subplots (79 m^2). Trees >1.37 m tall were identified by species, measured for diameter at breast height (DBH) to the nearest cm, and evaluated for crown ratio (the proportion of tree height which is canopy) to the nearest 10%.

Stand LAI was computed based on four of the leaf area algorithms by summing the leaf areas for all trees in the subplots and dividing by the appropriate area (i.e. entire plot or sum of subplot areas). Stand LAI could not be computed based on measured sapwood areas because not all trees in every stand were cored. For the LAI_{sabhr} stand-level estimates, the LAI_{DBH} algorithm was used for uncommon tree species and for trees of the three common species with DBH <12 cm. For application of the LAI_{sachz} algorithm at the stand level, tree height was first estimated from allometric equations on DBH (Table 6). In the case of Douglas-fir, age-class-specific linear regressions of DBH against height developed for the trees measured in this study were used. Species-specific allometric equations developed for trees from the Cascades Range in Oregon (Garman et al., 1995) were used for the other species.

Differences among the three age classes of stands in basal area, tree density, maximum DBH, mean DBH, and mean crown ratio were evaluated using one-way analysis of variance (SAS Institute Inc., 1990). Two-way analysis of variance was used for the comparisons among LAI estimation approaches within an age class, and among age classes for each LAI estimation approach.

3. Results

3.1. Tree-level

There were strong relationships between DBH and measured sapwood area for each species ($R^2 \geq 0.80$,

Table 6
Species-specific coefficients for relating diameter at breast height to tree height. The Douglas-fir relationships are from this study and those for the other species are from Garman et al., 1995

Species	Coefficient j	Coefficient k	Coefficient l	N	R^2
Douglas-fir [a]					
Young	6.4610	0.455	—	73	0.74
Mature	13.0740	0.439	—	34	0.78
Old-growth	25.5960	0.228	—	77	0.57
Western hemlock [b]	63.1314	−0.0163	1.0789	1006	0.91
Western redcedar [b]	56.9157	−0.0126	0.9359	545	0.88

[a] Height (m) = DBH × coefficient j + coefficient k.

[b] Height (m) = $1.37 + (\text{coefficient } j \times [1 - \exp(\text{coefficient } k \times \text{DBH})]^{\text{coefficient } l})$.

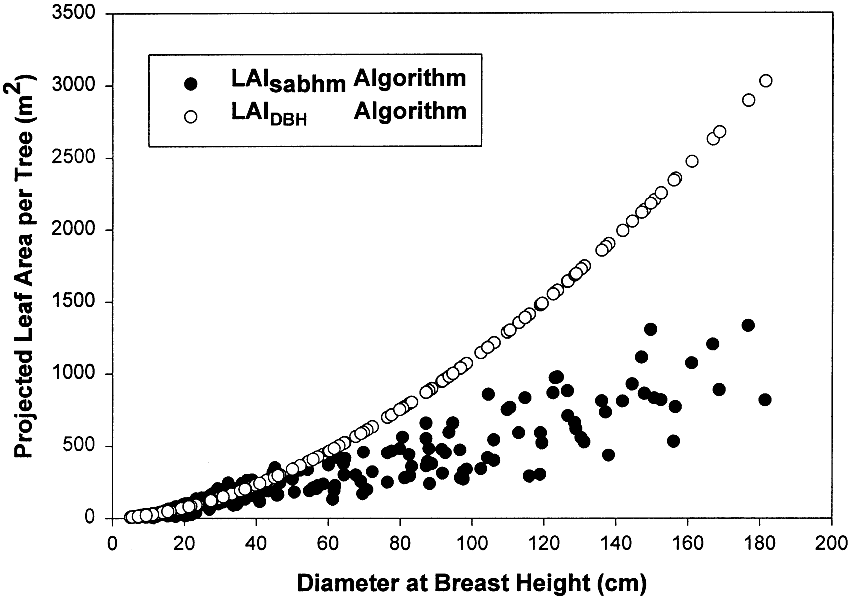

Fig. 2. Relationship of leaf area per tree for Douglas-fir trees estimated from measured sapwood area and from measured diameter at breast height. See Table 1 and Section 2 for specifics of $\mathrm{LAI}_{\mathrm{sabhm}}$ and $\mathrm{LAI}_{\mathrm{DBH}}$ algorithms.

Table 4). Neither crown ratio ($R^2 = 0.06$) nor the ratio of observed to expected tree height ($R^2 = 0.01$) were strongly related to the sign and magnitude of the residuals in the ratio of observed to predicted sapwood area.

For the cored Douglas-fir trees, estimates of leaf area per tree using $\mathrm{LAI}_{\mathrm{DBH}}$ and $\mathrm{LAI}_{\mathrm{sabhm}}$ were increasingly different as DBH increased (Fig. 2). In comparing tree-level estimates of $\mathrm{LAI}_{\mathrm{sabhr}}$ and $\mathrm{LAI}_{\mathrm{sabhz}}$, the latter tended to be higher at the larger DBHs (Fig. 3) but the difference was not as extreme as with $\mathrm{LAI}_{\mathrm{DBH}}$ (cf. Fig. 2 and note difference in y-axis scale). $\mathrm{LAI}_{\mathrm{sachz}}$ was lower than $\mathrm{LAI}_{\mathrm{sabhz}}$ when the crown ratio was <100% and the difference could be substantial (Fig. 4). For a Douglas-fir tree with DBH of 150 cm and crown ratio of 50%, the $\mathrm{LAI}_{\mathrm{sachz}}$ estimate was 44% less than the $\mathrm{LAI}_{\mathrm{sabhz}}$ estimate. For western hemlock and western redcedar, tree-level leaf area estimates showed a similar trend to that of Douglas-fir (Fig. 5). The relationships among the other algorithms were likewise similar to those of Douglas-fir and are not displayed.

3.2. Stand-level

All the structural characteristics examined differed among the age classes (Table 7). Mean basal area and maximum DBH was lowest in young stands and highest in old-growth stands. Tree density was highest in the young stands, intermediate in the old-growth stands, and lowest in the mature stands. Mean crown ratio was higher in young and old-growth stands than in mature stands.

At the stand level, the $\mathrm{LAI}_{\mathrm{DBH}}$ estimates ranged from 4.6 to 16.9 $\mathrm{m}^2\,\mathrm{m}^{-2}$ (Table 8). The $\mathrm{LAI}_{\mathrm{sabhr}}$ estimates were not significantly different than those for $\mathrm{LAI}_{\mathrm{DBH}}$ in the young stands but were consistently lower than the corresponding $\mathrm{LAI}_{\mathrm{DBH}}$ estimates in mature and old-growth stands. For $\mathrm{LAI}_{\mathrm{sabhz}}$, the maximum stand-level LAI was lower (14.0) and the minimum was higher (5.5 $\mathrm{m}^2\,\mathrm{m}^{-2}$) than $\mathrm{LAI}_{\mathrm{DBH}}$. The mean of the $\mathrm{LAI}_{\mathrm{sabhz}}$ estimates was similar to the $\mathrm{LAI}_{\mathrm{DBH}}$ in young and mature stands but markedly lower (24%) in the old-growth stands. The mean $\mathrm{LAI}_{\mathrm{sachz}}$ was lower than for $\mathrm{LAI}_{\mathrm{sabhz}}$ in all cases, particularly in the mature stands which had the lowest crown ratios.

For all the algorithms, LAI estimates increased from young to mature to old-growth stands although not all differences between age classes were significant. The differences between age-classes were greatest in the case of the $\mathrm{LAI}_{\mathrm{DBH}}$ approach where the

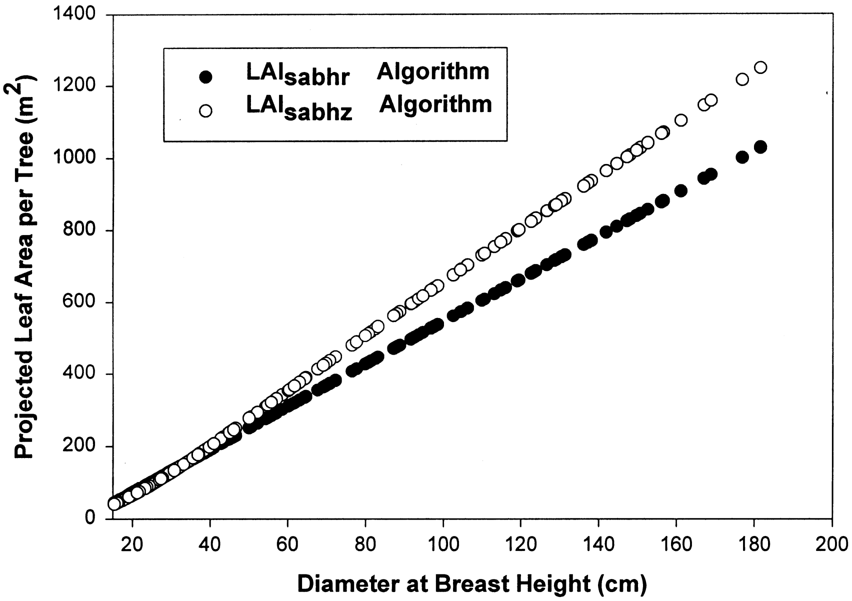

Fig. 3. Relationship of leaf area per tree for Douglas-fir trees estimated from a linear model derived from sapwood area measurements and from the algorithm for sapwood are at breast height in the ZELIG–PNW model. See Table 1 and Section 2 for specifics of LAI_{sabhr} and LAI_{sabhz} algorithms.

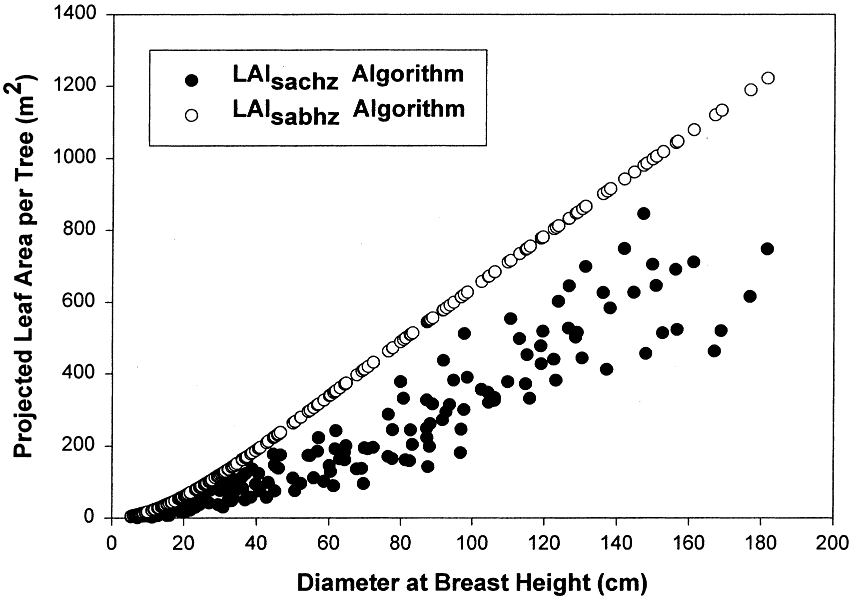

Fig. 4. Relationship of leaf area per tree for Douglas-fir trees estimated from the ZELIG–PNW model algorithm for sapwood area at breast height and from the ZELIG–PNW algorithm for sapwood area at the base of the crown. See Table 1 and Section 2 for specifics of LAI_{sabhz} and LAI_{sachz} algorithms.

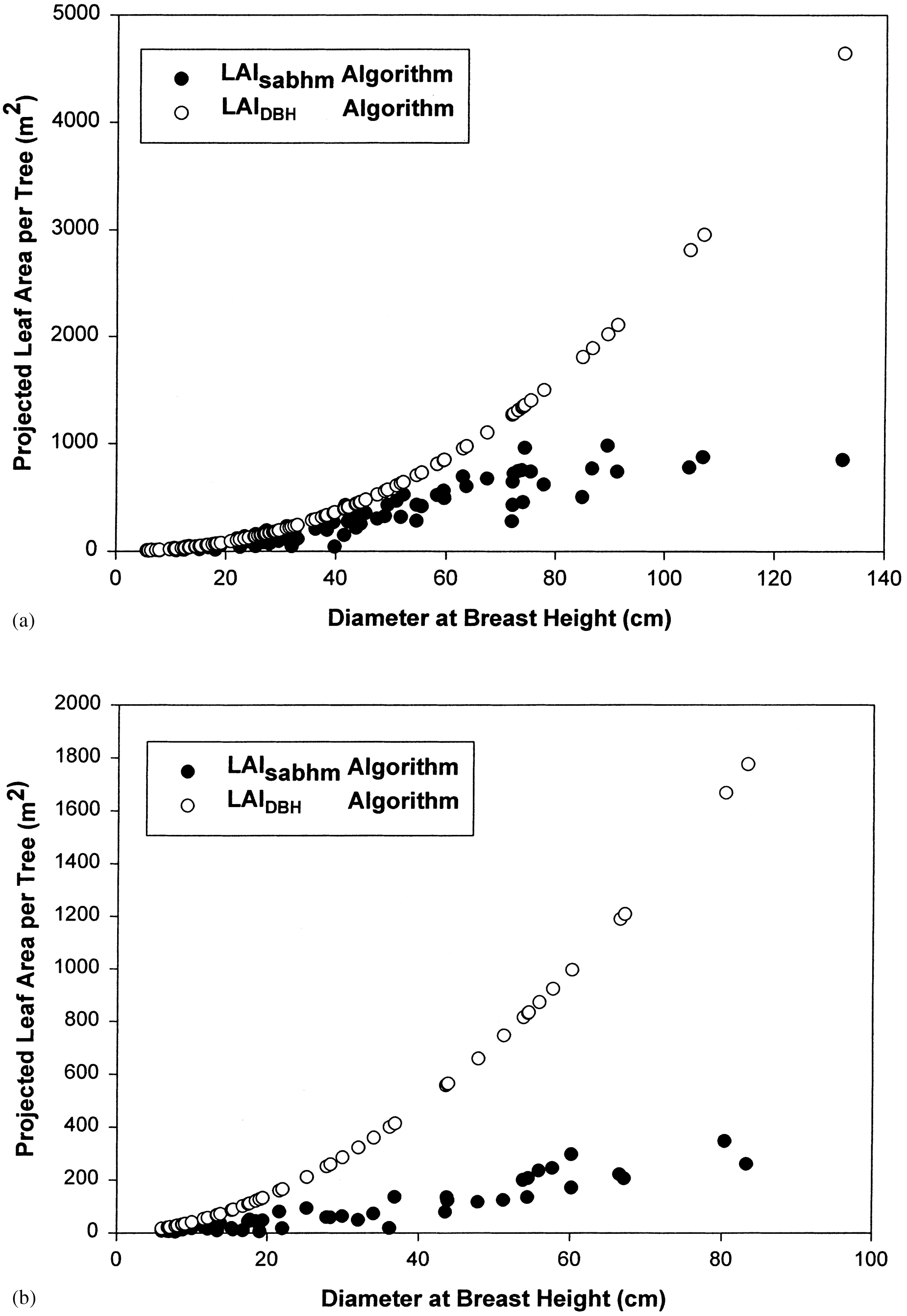

Fig. 5. Relationship of leaf area per tree for (a) western hemlock and (b) western redcedar trees estimated from measured sapwood area and from measured diameter at breast height. See Table 1 and Section 2 for specifics of LAI_{sabhm} and LAI_{DBH} algorithms.

average for the old-growth stands was nearly double that for the younger stands. The differences were smallest for the LAI_{sabhr} approach. The mean estimates for old-growth and mature stands in that case were still significantly higher than for the young stands.

Table 7
Stand characteristics

Age class	Basal area ($m^2 ha^{-1}$)	Density (trees ha^{-1})	Maximum DBH (cm)	Mean DBH (cm)	Mean crown ratio (%)
Young	24.2	1330	34	11	58
Young	20.9	1132	36	12	60
Young	26.3	2295	31	9	44
Average	23.8a	1586a	34a	11a	54a
Mature	63.8	212	94	57	38
Mature	69.1	368	79	46	33
Mature	46.1	340	57	25	34
Average	59.7b	307b	77b	43b	35b
Old-growth	76.2	656	173	18	56
Old-growth	91.6	624	148	25	37
Old-growth	84.6	360	110	44	50
Average	84.1c	547c	144c	29ab	48ab

Note: Averages across age classes sharing the same letters are not significantly different.

Table 8
LAI estimates by stand age class and alternative estimation method. LAI letters are from Table 1

Age class	LAI (dbh)	LAI (sabhr)	LAI (sabhz)	LAI (sachz)
Young	5.3	5.7	6.2	4.3
Young	4.6	5.1	5.5	3.7
Young	6.1	7.3	7.5	4.1
Average	5.3ab1	6.0b1	6.4b1	4.0a1
Mature	10.0	7.2	9.1	4.2
Mature	11.6	9.6	11.8	5.3
Mature	8.9	9.0	10.2	4.6
Average	10.2a2	8.6b2	10.4a2	4.7c1
Old-growth	15.7	7.8	10.8	7.6
Old-growth	15.5	9.2	11.7	7.5
Old-growth	16.9	10.7	14.0	8.5
Average	16.0a3	9.2c2	12.2b2	7.9d2

Note: Averages within age classes sharing the same letter are not significantly different ($p < 0.05$). Averages across age classes sharing the same number are not significantly different ($p < 0.05$).

4. Discussion

4.1. Tree-level leaf area estimates

The fact that the tree-level LAI_{DBH} and LAI_{sabhm} estimates agreed for small trees but not for large trees is consistent with previous work. For destructively sampled young Douglas-fir trees, the LAI_{DBH} and LAI_{sabhm} algorithms gave very similar estimates of leaf area in the study of Borghetti et al. (1986). Likewise, the difference observed here between LAI_{DBH} and LAI_{sabhm} for larger trees (50–100 cm DBH) was also found for the Douglas-fir trees studied by Peterson et al. (1987). The exponential form of the DBH-leaf biomass equation in the LAI_{DBH} algorithm probably becomes increasingly inappropriate for older trees due to structural considerations such as broken tops and low crown ratios.

Even in healthy intact trees, measurements of foliar biomass and leaf area made in large old-growth Douglas-fir trees at HJA (using extensive branch-level allometric measurements and associated destructive sampling) support lower estimates than are indicated by the LAI_{DBH} algorithm (Pike et al., 1977; Massman, 1982). For a representative tree of ca. 150 cm DBH, these studies indicate ca. 2850 m^2 per tree of needle surface area (1239 m^2 of projected leaf area), an estimate closer to that from the LAI_{sabhr} approach (~900 m^2) than the estimate from the LAI_{DBH} approach (~2000 m^2). For trees of 150 cm DBH, leaf area from the LAI_{sabhm} algorithm ranged from 500 to 1300 m^2.

A phase of rapidly increasing leaf area early in the life of a tree, as indicated by all algorithms, is consistent with increasing crown width and depth. However, if crown width stabilizes at some point after the onset of self-thinning, only the depth of the crown would continue to increase and even that would be constrained to some degree by the relatively low shade tolerance of Douglas-fir (Minore, 1979; Kuiper, 1988). The continued increase in leaf area would thus be moderated. The linear (as opposed to exponential) increase in measured sapwood area, and presumably leaf area, over the upper range of DBH for the Douglas-fir trees cored in this study supports this interpretation.

Observations along vertical profiles from breast height to the base of the crown in stems of Douglas-fir and other species have found significant reductions in sapwood area with height (Dean and Long, 1986; Maguire and Hahn, 1987; Maguire and Batista, 1996; but see also Long et al., 1981). Because $A_l : A_{sbh}$ and $A_l : A_{sch}$ may differ (Waring et al., 1982; Makela et al., 1995), leaf area estimates based on sapwood area at the base of the crown are potentially more accurate than those based on sapwood area at breast height. However, the practical difficulties of coring trees at the base of the crown limits direct measurement of sapwood area at the base of the crown for many applications. The alternative of estimating sapwood area at the base of the crown using allometry on DBH or sapwood area at breast height is feasible but introduces a number of other uncertainties.

First is that in the LAI_{sachz} formulation here, estimation of diameter or sapwood area at crown base relied on taper equations which may require site-specific parameterization. Maguire and Hahn (1987) developed taper equations for Douglas-fir trees in southwestern Oregon specifically for sapwood area and indicated that new parameterization would be required for trees of other regions. Secondly, the LAI_{sachz} approach assumes that sapwood width is constant with height to the base of the crown. In contrast, observations of vertical variation in sapwood width in Douglas-fir trees have found that the sapwood width may increase, decrease, or remain constant (Smith et al., 1966; J. Means, Oregon State University, unpublished).

An equally critical assumption with the LAI_{sachz} algorithm is that $A_l : A_{sch}$ is independent of crown ratio. Vertical profiles of sapwood area versus height in Douglas-fir trees show that sapwood area decreases continuously above breast height (Maguire and Batista, 1996) suggesting that the leaf area to sapwood area ratio is likewise changing continuously at least up to the base of the crown. This pattern would account for the generally higher $A_l : A_s$ reported at the base of the crown compared to breast height (Waring et al., 1982) and a predicted increase in sapwood permeability with height in the model of Pothier et al. (1989). It also suggests that $A_l : A_{sch}$ may depend on crown ratio. The trees in the mature and old-growth stands studied here were much larger than those in the Waring et al. (1982) study which defined the difference in $A_l : A_s$ between breast height and the base of the crown for the LAI_{sachz} algorithm. If that ratio is larger at greater heights and lower crown ratios, then the LAI_{sachz} estimates may have been too low.

4.2. Stand-level LAI estimates

Forest productivity models, such as Forest-BGC (Running and Coughlan, 1988), are typically not particularly sensitive to differences in LAI between 8 and 16 in terms of light absorption; at an LAI of 8, over 95% of the photosynthetically active radiation is considered absorbed by the canopy. However, if foliar biomass for model initialization is calculated from LAI and specific leaf area, an overestimate of LAI can lead to an overestimate of foliar biomass and hence foliar respiration, with more significant impacts on NPP estimates. Thus, the ability to measure LAI accurately in stands with high LAI is important.

Among the sapwood area-based algorithms, the LAI_{sabhr} estimates for individual stands were consistently lower than the associated LAI_{sabhz} estimates. The difference was greatest in the old-growth stands because the bias towards higher sapwood area estimates using the LAI_{sabhz} was most evident in the larger trees. The bias found here in predicted A_{sbh} using the regional parameterization of the DBH-sapwood width equation suggests that local information on DBH-sapwood area relationships may be needed for maximum accuracy. Considering the scatter around the DBH-sapwood area regression, the optimal situation would be to core all the large trees in a stand rather than relying on a statistical relationship of sapwood width or area to DBH.

The differences between the stand-level LAI_{sabhz} and LAI_{sachz} estimates are primarily a function of the crown ratios for trees within a stand. Crown ratios are often <50% in these closed conifer forests, and the LAI_{sachz} approach resulted in mean LAI estimates

35% lower than for LAI_{sabhz} in old-growth stands, 55% lower in mature stands, and 37% lower in the young stands. As noted, the magnitude of this reduction may be overestimated if $A_l : A_{sch}$ varies as a function of tree height and crown ratio.

For all the algorithms, there was a significantly higher mean LAI in older than in younger stands. Because mature to old stands in other temperate zone conifer forests often have the same or lower LAI than younger closed canopy stands (Waring and Schlesinger, 1985; Ryan and Waring, 1992; Binkley et al., 1995; Gower et al., 1996; Mencuccini and Grace, 1996; Ryan et al., 1997), it will be important to continue efforts to measure LAI accurately enough for confirmation of the possibility of higher LAIs in older stands in the PNW. Various mechanism to account for different trends in LAI among different conifer forest types, such as an increasing proportion of the foliage from shade tolerant species, might then be explored.

4.3. Comparisons to LAI estimates from litterfall

Litterfall can provide a more direct estimate of LAI than allometric approaches. If the foliar biomass of a stand is in steady state, then the total amount of foliar biomass is the product of the needle retention time (NRT) and the annual litterfall. If values of specific leaf area are known, foliar biomass estimates can be converted to all-sided leaf area, and hence to LAI. The limitations of this approach include climate-related interannual variability in litterfall (Trofymow et al., 1991), variation in specific leaf area with depth in the canopy (Niinemets, 1997), and variation among species and sites in NRT (Reich et al., 1995).

At HJA, several litterfall studies have been conducted in mature to old-growth stands where the assumption of a steady state in LAI is most likely to be valid. In one study, litterfall was collected monthly for four years at seven of the reference stands associated with the HJA Long Term Ecological Research program (Hawk et al., 1978; Van Cleve and Martin, 1991). Litterfall varied by as much as a one-third from year to year at a given stand but the range in the four-year average across stands was relatively small (e.g. 152–206 g m^{-2} $year^{-1}$ for needle litter). The overall mean for needle litterfall was 171 g m^{-2} $year^{-1}$ and for other leaf material was 4 g m^{-2} $year^{-1}$. This value for needle litterfall is close to those from other studies at HJA including the 190–236 g m^{-2} $year^{-1}$ reported for needle litterfall in several stands by McShane et al. (1983), the mean for five old-growth stands of 174 g m^{-2} $year^{-1}$ from Grier and Logan (1977), and 186 g m^{-2} $year^{-1}$ reported for an old-growth stand by Sollins et al. (1980).

If annual needle litterfall in older stands is thus assumed to be ca. 180 g m^{-2} $year^{-1}$, mean NRT is assumed to be five years (Fujimori et al., 1976; Pike et al., 1977), and average specific leaf area (all-sided) is assumed to be 174 cm^2/g (Gholz et al., 1976; Marshall and Waring, 1986), the estimated total leaf area is 15.6 m^2 m^{-2} and projected leaf area is 6.8 m^2 m^{-2}. Mean NRT could be higher in these stands since Douglas-fir needles can be retained as long as 10 years (Pike et al., 1977). However, the NRT for hemlock is of the order of 4–5 years (M. Harmon, Oregon State University, personal communication) and hemlock is well represented in the three old-growth stands studied here, so the canopy average is unlikely to be much higher than five years. If the canopy average NRT is raised to six years, the estimated canopy LAI rises to 8.3 m^2 m^{-2}. The canopy average specific leaf area for an old-growth stand may also be somewhat higher since the SLA for hemlock at two stands in HJA averaged 204 cm^2 g^{-1} (Gholz et al., 1976), 17% higher than that for Douglas-fir in the same study. SLA also tends to be higher in more shaded foliage, deeper in the canopy (Borghetti et al., 1986; Niinemets, 1997), and a deep canopy is a characteristic feature of old-growth Douglas-fir stands (Franklin and Spies, 1991). Considering all these factors, the litterfall studies support LAI estimates of the order of 7–10 m^2 m^{-2} in these older stands, results most consistent with the LAI_{sabhr} algorithm.

4.4. Operational estimation of LAI

Results here strongly suggest that the LAI_{DBH} algorithm overestimates LAI in older Douglas-fir stands. Old-growth stands will continue to be an important part of the managed forest landscape in the Pacific Northwest (e.g. U.S.D.A. Forest Service and U.S.D.I. Bureau of Land Management, 1994) and are of interest for understanding patterns in ecosystem structure and function over the course of succession.

The $\mathrm{LAI}_{\mathrm{DBH}}$ algorithm is also problematic from a number of other perspectives, including variation in the relevant species-specific coefficients associated with site nutrient availability (Grier et al., 1984; Gower et al., in press).

Allometric studies which have demonstrated a linear relationship of A_l and A_s, and the observed responsiveness of sapwood area at breast height to imposed changes in crown ratio and leaf area (Margolis et al., 1988), confirm that sapwood area carries significant information about leaf area. An important research question is whether that information remains useful in the face of variability in $A_l : A_s$, i.e., is the variability small enough to be ignored for some purposes, or are there statistical approaches which might permit appropriate adjustments? The clearest departure from a fixed $A_l : A_s$ is in the case of variation in tree vigor: faster growing trees often have wider annual rings and higher $A_l : A_s$ (Bancalari et al., 1987). Ring width at a given age might thus be used as a covariate in equations relating A_l to A_s (e.g. Albrektsson, 1984). Relatively xeric climates have been associated with lower $A_l : A_s$ within some species (Callaway et al., 1994; Mencuccini and Grace, 1995) and in this case a drought index (e.g. annual precipitation minus annual potential evapo-transpiration) could serve to modify a base ratio. Stand density and tree crown characteristics may also alter $A_l : A_s$ in consistent ways (Dean et al., 1988; Long and Smith, 1988; Thompson, 1989) and could therefore potentially be used in predictive equations. Lastly, increasing tree height is thought to be associated with decreasing hydraulic conductance which may in turn decrease $A_l : A_s$ (Ryan and Yoder, 1997). Consequently, tree height might provide an important index to the degree of departure from $A_l : A_s$ at some reference height.

The primary alternative to the allometric algorithms for LAI are based on light interception. The ease of sampling makes optical approaches attractive. However, potential problems include quantifying the amount of light scattered by branches, the issue of branch clumping, and accounting for horizontal heterogeneity (Fassnacht et al., 1994; Gower et al., in press). Optimally, prior to development of empirical models for prediction of LAI from remote sensing imagery for a particular region, optical methods could be calibrated to sapwood-area- or litterfall-based methods over a range of stand ages for appropriate forest types. Optical methods could then be used to survey a large number of plots.

5. Conclusions

A reliable means for estimating stand-level LAI over the complete range of LAI on a landscape is needed for parameterization and validation of forest ecosystem and hydrology models and remote sensing-based approaches to mapping LAI. Alternative allometric approaches to estimating LAI in Douglas-fir forests in the Pacific Northwest yielded similar results for young stands but significantly different LAI estimates in older stands. Earlier studies of individual old trees, and estimates of stand-level LAI from litterfall, support the lower estimates in older stands associated with algorithms based on sapwood area. The limitations of the sapwood area-based approaches include the impracticality of measuring sapwood on all trees in a stand, uncertainties in predicting sapwood area from other measurements such as DBH, and variability in the leaf area to sapwood area ratio. Because of significant uncertainties associated with all approaches to measurement of LAI in mature to old-growth Douglas-fir forests, there is a need to compare sapwood area, litterfall, and optical methods (e.g. Chen et al., 1997).

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