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ORIGINAL ARTICLE

Branch surface area and its vertical distribution in coastal Douglas-fir

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Abstract Wood area index (WAI; total surface area of branches and bole per unit of land area) is an important yet often neglected forest structural attribute. Branchwood surface area, in particular, has significant implications for many ecophysiological processes including total respiration and interception of radiation and rainfall. Branch surface area was estimated at the branch-, tree-, and stand-level for 33 Douglas-fir (*Pseduotsuga menziesii* [Mirb.] Franco) plantations in the Oregon Coast Range. Patterns in WAI, leaf area index (LAI; total surface area of needles per unit of land area), tree area index (TAI = WAI + LAI) and various ratios of these dimensions were then investigated. The main axes of primary branches (those attached to the main stem) comprised 82 ± 13% of total branchwood surface area. Tree surface area (needles + woody tissue) increased with increasing tree size and crown length, and decreased with greater intensity of Swiss needle cast (SNC). At the stand-level, woody surface area increased with greater stand density and decreased with more severe SNC, but on average it constituted 29 ± 12% of total tree surface area. Branchwood surface area and bole surface area contributed equally to WAI. The variation in WAI for a given LAI has important implications for radiation and rainfall attenuation in these stands and for accurate partitioning of intercepted radiation between photosynthetic and non-photosynthetic tissues.

Keywords Branch surface area · Crown structure · Wood area index · Swiss needle cast · Douglas-fir

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Introduction

Wood area index (WAI; total surface area of branches and the tree bole) has received significantly less attention than leaf area index (LAI; total surface area of foliage per unit of land area) as an attribute of forest structure. The magnitude of WAI, however, has important implications for total radiation absorption by the canopy (Oker-Blom et al. 1991), for the partitioning of intercepted radiation by photosynthetic vs. non-photosynthetic tissues, and for accurately determining LAI through indirect measurement (Bréda 2003). WAI has been estimated for relatively few species, and its apparent contribution to tree area index (TAI = WAI + LAI) was found to vary from 7 to 41% (Bréda 2003). Little is currently known about how WAI varies within a species, particularly with respect to changes in site quality, stand age, and stand density, and in response to silvicultural manipulation of various stand structural features.

The surface area of branches is one of the most difficult components of WAI to determine accurately because branch structure and crown architecture vary widely, even among trees of similar size (diameter and height). Because branches have been assumed to intercept a relatively small amount of direct beam radiation in both coniferous and deciduous forests (Fassnacht et al. 1994; Kucharik et al. 1998), branchwood surface area has not been explicitly included in most indirect assessments of LAI or canopy net photosynthesis models. Branchwood surface area, however, plays a role in several other ecological processes, including maintenance respiration rates (Bosc et al. 2003), rainfall storage capacity (Keim 2004), avian foraging behavior (Doster and James 1998; Pierce and Grubb 1981), and spruce budworm infestation level (Jones 1979). Branchwood surface area and its vertical distribution also have important implications for forest biodiversity, particularly as a substrate for epiphytic bryophytes, lichens, fungi, and invertebrates (e.g. Ingram and Nadkarni 1993).

Branch surface area has been estimated in a variety of ways. Whittaker and Woodwell (1967) presented an equation based on branch divarication theory using measurements of branch basal diameter, branch length, the number of current twigs as branch termini, and mean diameter of current twigs. Jennings et al. (1990) computed branch surface area as the area of a triangle with a height and base corresponding to length and maximum width, respectively. Both Halldin (1985) and Baldwin et al. (1997) assumed allometric relationships between branch diameter and surface area, while Mohren (1987) used a fixed value of 0.3 m^2 kg^{-1}, to predict branch surface area at the branch- and tree-level. These authors, however, do not report how sample branch surface area was actually measured. Halldin (1985) and Baldwin et al. (1997) are apparently the only authors to examine patterns in the vertical distribution of branchwood surface area for a subject stand. Despite the variety of methods for estimating branchwood surface area, these previous studies have limited applicability due to their relatively small sample sizes and lack of replication across the landscape.

The goal of this research was to improve estimates of radiation and rainfall interception in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) plantations, and thereby facilitate more accurate forecasting of plantation productivity under alternative silvicultural regimes and under differing levels of Swiss needle cast (SNC). Approximately 72,000 ha of Douglas-fir plantations in the Oregon Coast Range are currently showing symptoms of SNC (Kanaskie et al. 2004), a foliar disease leading to premature needle abscission, wide variation in crown condition, and stand LAIs ranging from 3 to 10 (Weiskittel 2003). These plantations are also managed under a wide variety of silvicultural regimes, producing equally large differences in stand structure. The objectives of this paper, therefore, were: (1) to assess the variability in WAI among Douglas-fir plantations in north coastal Oregon; (2) to relate WAI to site and stand structural conditions; and (3) test the hypothesis that the ratio of needle area to woody surface area declines with increasing SNC severity. Achieving these objectives required development of equations for predicting branch surface area at the individual branch-, tree-, and stand-levels (Table 1).

Table 1 Symbols, definitions and units of variables for characterizing woody surface area of Douglas-fir plantations

Symbol	Definition	Unit
a	Beta parameter	–
A_i	Indicator variable for age class i ($i = 1, 2, 3, 4, 5+$)	–
AGE	Stand mean breast-height age	years
b	Beta parameter	–
BAI	Branchwood area index (total surface area)	m^2 m^{-2}
BA_{DF}	Plot basal area in Douglas-fir	m^2 ha^{-1}
$\%BA_{DF}$	Proportion of plot basal area in Douglas-fir (0–1)	%
BD	Branch diameter	mm
BHT	Branch height in the tree	m
BL	Branch length	m
BSA	Total branch surface area	cm^2
CL	Crown length	m
CR	Crown ratio	–
CLSA	Crown sparseness index	cm cm^{-2}
d_l	Diameter of primary branch axis at distance l from the branch tip	mm
DBH	Diameter at breast height	cm
DIN_CAN	Branch depth into the canopy (maximum plot tree height – branch height)	m
HCM	Height to crown midpoint	m
HT	Total tree height	m
FOLRET	Plot mean foliage retention	years
l	Distance from bole along primary branch axis	m
TAI	Tree area index (LAI + BAI + SAI)	m^2 m^{-2}
SAI	Stem area index	m^2 m^{-2}
SI	Estimated Bruce's (1981) plot site index	m at 50-year
TBSA	Surface area of all branches on a tree	m^2
TLBSA	Surface area of lateral shoots on a tree	m^2
PRISA	Surface area of all primary branch axes on a tree	m^2
TOPHT	Plot top height (mean HT of the 100 largest trees per ha)	m
TPH	Trees per ha	–
WAI	Total wood area index (BAI + SAI)	m^2 m^{-2}
Z	Relative position along the primary branch axis, l/BL	–

Table 2 Attributes of the 33 plots sampled for estimating woody surface area in Douglas-fir plantations

Attribute	Mean	Standard deviation	Minimum	Maximum
Douglas-fir basal area (m^2 ha^{-1})	32.2	14.1	10.0	72.6
Douglas-fir trees per ha	535	267	150	1223
Douglas-fir quadratic mean diameter (cm)	30.0	10.7	11.4	53.5
Douglas-fir relative density (Curtis 1982) (m^2 ha^{-1} $cm^{-1/2}$)	5.82	1.81	2.95	10.09
% Basal area in other conifer	7	12	0	53
% Basal area in hardwoods	2	2	0	9
Total basal area (m^2 ha^{-1})	36.9	14.5	10.4	76.8
Average breast-height age (year)	29	15	11	62
Average foliage retention (year)	2.5	0.8	1.3	4.4
Bruce's (1981) site index (m of top height at 50 years breast height age)	39	4	27	46
Crown sparseness index (cm cm^{-2})	5.83	1.22	3.61	8.14
Distance from the coast (km)	16.6	11.9	1.0	53.0
Elevation (m)	218	143	24	549

Materials and methods

Field work

The sample collected for this study consisted of 122 Douglas-fir trees from 33 plantations across the northern Oregon Coast Range, north of Newport (N44°40′, W124°4′) and south of Astoria (N46°7′, W123°45′). Breast height age ranged from 10 to 60 years and SNC varied from mild to severe as measured by foliage retention (Table 2). In the spring of 2002 and 2003, foliage retention (years) was determined in each third of the live crown with the aid of binoculars. Plot-level SNC intensity was indexed by the average foliage retention for all three crown levels in ten sample trees per stand. Ratings from 2002 were used for plots sampled in the fall of that year, and ratings from 2003 were used for plots sampled in the winter of 2003. Weiskittel et al. (2006) give a more complete description of the study sites and sampling scheme.

In each stand, three to five trees were felled and intensively measured. Before felling, diameter at breast height (DBH), total height (HT), height to crown base (HCB), and maximum crown width (CW) were measured (Table 3). After felling, a disk was cut from the bole at crown base and sapwood cross-sectional area was estimated by measuring sapwood widths on the longest and perpendicular-to-longest axes and assuming elliptical total and heartwood cross-sections. In addition, the height and diameter (just beyond basal swell) of every living primary branch (those attached to the tree bole and >1 mm in diameter) were determined. Ten to fifteen branches (3–5 per crown third, including 2–3 whorl and 1–2 interwhorl branches) were randomly selected and transported back to the laboratory (Table 4).

Laboratory work

The 668 sample branches were clipped into separate age classes, placed into smaller paper bags, and oven dried at 85°C for 3 days. The needles were separated from the woody material, and each component was weighed to the nearest 0.01 g. The main axis of each primary branch was also cut into age classes, dried and weighed. Each annual segment of the branch main axis was measured for distance from the branch tip, total length, and midpoint diameter.

Specific shoot area (SSA) of secondary and higher order shoots (hereafter referred to as lateral shoots) was required to convert lateral shoot mass to lateral shoot surface area. On 309 branches selected from the 668 available, five to ten higher order shoots of each age class were measured for length and midpoint diameter. Surface area was then

Table 3 Attributes of the 122 trees sampled for estimating woody surface area of individual Douglas-fir trees

Attribute	Mean	Standard deviation	Minimum	Maximum
DBH (cm)	30.4	10.2	12.5	66.6
Height (m)	23.95	7.89	11.90	45.80
Height to live crown (m)	10.02	5.83	0.50	28.33
Crown length (m)	13.78	3.59	6.96	27.20
Crown ratio	0.61	0.13	0.23	0.96
Crown sparseness (cm cm^{-2})	6.92	3.85	2.15	34.94
Surface area of primary branch axes (m^2)	17.34	10.41	4.13	66.61
Surface area of lateral (secondary and higher order) shoots (m^2)	5.32	3.37	0.48	15.91

Table 4 Attributes of the 668 branches sampled for estimating woody surface area of individual Douglas-fir branches

Attribute	Mean	Standard deviation	Minimum	Maximum
Diameter (mm)	21.0	12.3	1.7	63.9
Total length (m)	1.95	1.21	0.08	6.09
Total foliated length (m)	1.58	0.97	0.08	4.83
Depth in crown (m)	6.64	4.39	0.27	27.25
Branch height above ground (m)	22.70	8.63	1.71	44.29
Depth into canopy (m)	11.41	5.25	0.94	28.47
Surface area of primary branch axis (cm^2)	1465.62	1475.72	4.28	8086.07
Surface area of lateral shoots (cm^2)	334.94	360.66	0.00	1481.82
% Lateral shoot surface area in foliated 1-year-age class	20	21	0	100
% Lateral shoot surface area in foliated 2-year-age class	26	17	0	77
% Lateral shoot surface area in foliated 3-year-age class	14	11	0	89
% Lateral shoot surface area in foliated 4-year-age class	9	7	0	96
% Lateral shoot surface area unfoliated	31	29	0	97

calculated as the frustrum of a cone, and SSA ($cm^2\ g^{-1}$) of each age class was calculated as the ratio of surface area of the sample shoots to their dry weight. Lateral shoot surface area of all 668 sample branches was obtained as the product of total dry weight for a given age class of lateral shoots and SSA estimated from branch-level attributes (see Analysis approach section). Branchwood surface areas included both foliated and unfoliated portions of the branch, but did not include foliage area.

Analysis approach

Various linear and nonlinear regression models were fitted to the data to develop branch-, tree-, and stand-level equations. Final models were chosen on the basis of biological expectation (to avoid spurious relationships), residual analysis (to meet the assumptions of linear regression), likelihood ratio tests (to compare nested model forms), and Akaike's information criterion (AIC; to ensure model parsimony). Further, due to the large dataset used in this analysis and the increased probability of multicollinearity, variance inflation factors of the primary covariates were assessed. Multilevel random effects were utilized to address the hierarchical nature of the dataset (i.e., branch within tree within plot) and weights were estimated by a power variance function to correct for heteroskedasticity when appropriate. All analyses were done in SAS v8.2 (SAS Institute, Cary, NC) and S-PLUS v6.2 (Mathsoft, Seattle, WA). Response and predictor variables represent a variety of levels from the hierarchical sampling scheme, including plot, tree, branch, and age class (Table 4).

Branch-level analysis

Specific shoot area (SSA) was regressed on a set of predictor variables known to influence this ratio:

$$\log(\mathrm{SSA}) = \beta_{10} + \beta_{11}A_1 + \beta_{12}A_2 + \beta_{13}A_3 + \beta_{14}A_4 + \beta_{15}\mathrm{DIN\_CAN} + \beta_{16}\mathrm{BD} + \beta_{17}\mathrm{CL} + \tau_1 + \gamma_1 + \varepsilon_1 \quad (1)$$

where A_i is an indicator variable for age class i ($i = 1, 2, 3, 4$), DIN_CAN is branch depth into the canopy (m; maximum stand height − branch height), BD is branch diameter (mm), CL is crown length (m; tree height − height of lowest live branch), the β_{1k} are parameters to be estimated from the data, τ_1 is a random plot effect with $\tau_1 \sim N(0, \sigma_{\tau 1}{}^2)$, γ_1 is a random tree effect with $\gamma_1 \sim N(0, \sigma_{\gamma 1}{}^2)$, and ε_1 is a random disturbance with $\varepsilon_1 \sim N(0, \sigma \varepsilon_1{}^2)$. SSA predicted from this model was used to convert weight of lateral shoots to area of lateral shoots on each sample branch. All estimates of SSA from this model were corrected for log bias with the naïve estimator discussed by Flewelling and Pienaar (1981).

Surface area of the primary branch axis was estimated by fitting and numerically integrating the following variable-exponent taper equation (Kozak 1988):

$$d_i = \beta_{20}\mathrm{BD}^{\beta_{21}} \left(\frac{1-\sqrt{Z}}{1-\sqrt{0.2}}\right)^{\beta_{22}\sqrt{Z}+Z^{\beta_{23}}+\beta_{24}\log(Z)+\beta_{25}\exp(Z)+\beta_{26}\left(\frac{\mathrm{BD}}{\mathrm{BL}}\right)} + \tau_2 + \gamma_2 + \varepsilon_2 \quad (2)$$

where d is diameter outside bark (mm) on the primary branch at a distance l_i from the branch tip (m), BD is defined above, Z is the relative distance from branch base (l_i/BL), the β_{2k} are parameters to be estimated from the data, τ_2 is a random plot effect with $\tau_2 \sim N(0, \sigma_{\tau 2}{}^2)$, γ_2 is a random tree effect with $\gamma_2 \sim N(0, \sigma_{\gamma 2}{}^2)$, and ε_2 is a random disturbance with $\varepsilon_2 \sim N(0, \sigma\ \varepsilon_2{}^2)$. Total surface area of each sample branch was calculated as the sum of the primary branch axis and all secondary and higher order lateral shoots.

Estimation of branchwood surface area on the 122 sample trees required prediction of surface area for all the branches on branch diameter and height. Total foliage mass on a branch has been shown to vary by diameter and relative height in the crown (Xu and Harrington 1998; Weiskittel et al. 2006), and individual branch mass and surface area were expected to follow a similar pattern. The following equation was therefore fitted to the data representing the 668 sample branches:

$$\mathrm{BSA} = \beta_{30}\mathrm{BD}^{\beta_{31}} \exp\left(\beta_{32}\frac{\mathrm{BHT}}{\mathrm{HT}} + \beta_{33}\mathrm{SI}\right) + \tau_3 + \gamma_3 + \varepsilon_3 \quad (3)$$

where BSA is total branch surface area (cm^2), BHT is branch height from ground (m), HT is total tree height (m), SI is Bruce's (1981) site index (top height in meters at 50 years), the β_{3k} are parameters to be estimated from the data, τ_3 is a random plot effect with $\tau_3 \sim N(0, \sigma_{\tau 3}{}^2)$, γ_3 is a random tree effect with $\gamma_3 \sim N(0, \sigma_{\gamma 3}{}^2)$, and ε_3 is a random disturbance with $\varepsilon_3 \sim N(0, \sigma\varepsilon_3{}^2)$.

Tree-level analysis

The plot- and tree-specific random effects were included in Eq. (3) to predict total surface area of each branch on all 122 intensively measured sample trees, similar to the procedure outlined by Robinson and Wykoff (2004) for imputing missing tree heights. The predicted surface areas for all the branches were summed to estimate total branchwood surface area for each tree. A system of equations (Kmenta 1997) was then fitted to the data to produce a prediction system for tree branchwood surface area and its components (surface area of the primary branch axis and lateral shoot surface area):

$$\begin{aligned}
\mathrm{TPRISA} &= \exp(\beta_{400} + \beta_{401}\mathrm{DBH} + \beta_{402}\mathrm{CL} + \beta_{403}\mathrm{CR} + \beta_{404}\mathrm{CLSA}) + \varepsilon_{41} \\
\mathrm{TLBSA} &= \exp(\beta_{405} + \beta_{406}\mathrm{DBH} + \beta_{407}\mathrm{CL} + \beta_{408}\mathrm{CR} + \beta_{410}\mathrm{CLSA}) + \varepsilon_{42} \\
\mathrm{TBSA} &= \exp(\beta_{411} + \beta_{412}\mathrm{DBH} + \beta_{413}\mathrm{CL} + \beta_{414}\mathrm{CR} + \beta_{415}\mathrm{CLSA}) + \varepsilon_{43}
\end{aligned} \quad (4)$$

where TPRISA is surface area of the primary branch axis (cm^2), TLBSA is lateral shoot surface area (cm^2), TBSA is total branch surface area (cm^2), CR is crown ratio (CL/HT), CLSA is a crown sparseness index indicating SNC severity (ratio of live crown length to sapwood area at crown base, cm cm^{-2}; Maguire and Kanaskie 2002), the β_{4k} are parameters to be estimated from the data, and $\varepsilon_{4j} \sim N(0, \sigma_{4j}{}^2)$. A constraint was placed on the system to ensure additivity of the components (e.g. Parresol 2001).

The vertical distribution of branchwood surface area was characterized on the felled trees by dividing the crown into ten segments of equal length and summing the estimated branchwood surface area within each segment. A standard two-parameter beta distribution was fitted to the empirical distribution for each tree, resulting in estimates of two parameters, *a* and *b*, for each tree. A separate beta distribution was fitted for total branchwood surface area, primary branch axis surface area, and lateral shoot surface area.

The effects of tree dimensions and SNC intensity on the vertical distribution of branchwood surface area were tested by regressing the estimated beta parameters on potential predictors that included indices of SNC severity. Parameters in the following system of equations were estimated by seemingly unrelated regression to account for cross-equation correlation (Kmenta 1997):

$$\begin{aligned}
a_i &= \beta_{50i} + \beta_{51i}\mathrm{HCM} + \beta_{52i}\mathrm{CLSA} + \beta_{53i}\mathrm{RD_{DF}} + \beta_{54i}\mathrm{SI} + \varepsilon_{51i} \\
b_i &= \beta_{55i} + \beta_{56i}\mathrm{HT} + \beta_{57i}\mathrm{HCM} + \beta_{58i}\mathrm{CL} + \beta_{59i}\mathrm{TOPHT} + \varepsilon_{52i}
\end{aligned} \quad (5)$$

where a_i is the *a*-parameter for total branchwood surface area ($i =$ BSA), primary branch axis surface ($i =$ PRISA), or lateral shoot surface area ($i =$ LBSA), b_i is the b-parameter for the respective surface areas, HCM is the height to crown midpoint, $\mathrm{RD_{DF}}$ is Douglas-fir relative stand density (Curtis 1982), TOPHT is stand top height (m), the β_{5ki}s are parameters to be estimated from the data, $\varepsilon_{5ki} \sim N(0, \sigma_{5i}{}^2)$, and all other variables are defined as above.

The implied vertical distribution of branchwood surface area was estimated for a tree of average size across the range in conditions covered by this study to provide a graphical assessment of differences in surface area distribution for total branchwood, primary branch axis, and lateral shoots.

Stand-level analysis

As in the tree-level analysis, random plot effects were included to estimate total branchwood surface area for each plot tree using Eq. (4). In addition, stem area was estimated by integration of a taper equation developed for SNC impacted Douglas-fir (Weiskittel and Maguire 2004). Both branchwood area and stem area were then expressed as a ratio to occupied ground area, analogous to leaf area index (LAI). A system of equations (Kmenta 1997) was then fitted to describe the effect of SNC intensity (and other covariates) on branchwood area index (BAI) and stem area index

(SAI):

$$\mathrm{BAI} = \exp(\beta_{600} + \beta_{601}\mathrm{AGE} + \beta_{602}\mathrm{TOPHT} + \beta_{603}\mathrm{FOLRET}) + \varepsilon_{61}$$

$$\mathrm{SAI} = \exp(\beta_{604} + \beta_{605}\mathrm{TOPHT} + \beta_{606}\mathrm{RD}_{\mathrm{DF}} + \beta_{607}\mathrm{FOLRET}) + \varepsilon_{62} \quad (6)$$

where AGE is total stand age, FOLRET is mean plot foliage retention as an index of SNC severity, the β_{6k} are parameters to be estimated from the data, and $\varepsilon_{6k} \sim N(0, \sigma_{6k}^2)$. Previous estimates of projected leaf area index (LAI) for these plots (Weiskittel 2003) were converted to all-sided LAI using the values provided in Barclay and Goodman (2000). Tree surface area index (TAI) was estimated as the sum of leaf, branchwood, and stem surface areas. The trend in TAI across the examined stand conditions was described with the following equation:

$$\ln(\mathrm{TAI}) = \beta_{70} + \beta_{71}\mathrm{RD}_{\mathrm{DF}} + \beta_{72}\%\mathrm{BA}_{\mathrm{DF}} + \beta_{73}\mathrm{AGE} + \beta_{74}\mathrm{FOLRET} + \varepsilon_7 \quad (7)$$

where $\%\mathrm{BA}_{\mathrm{DF}}$ is the percent stand basal area in Douglas-fir, $\varepsilon_7 \sim N(0, \sigma_7^2)$, and all other variables were defined above.

Results

Branch-level

Specific shoot area averaged 2.44 ± 1.29 cm^2 g^{-1}, but generally increased over successively older age classes (Tables 5 and 6). For a given age class, SSA increased with greater depth into the canopy and decreased with increasing branch diameter and crown length (Table 6). Specific shoot area of the 4-year age class did not differ significantly from that of the ≥ 5-year age class. Unfoliated shoots comprised a significant portion of the lateral shoot surface area (Table 4).

Branch profile was described well by the variable-exponent taper equation ($R^2 = 0.91$; Table 6). Mean bias and mean absolute bias of the equation were 0.36 ± 3.66 mm and 2.31 ± 2.86 mm, respectively. The basal swell of branches led to slight under-prediction of branch diameter near point of insertion into the bole. Branch taper was not significantly affected by foliated branch length or depth into the canopy. Surface area of the primary branch axis ranged from 4 to 8086 cm^2 (Table 4) and comprised on average $82 \pm 13\%$ of total branch surface area.

Total branch surface area (BSA) increased monotonically with greater branch diameter and site index, but decreased with higher relative position within crown. Surface area of the primary branch axis and lateral shoots amounted to $14 \pm 7\%$ and $4 \pm 2\%$, respectively, of the foliage area on the same branch.

Tree-level

Total surface area of branchwood on individual trees averaged 22.5 ± 12.8 m^2, and $77 \pm 8\%$ of this total was contributed by primary branch axes. The total amount of branchwood surface area on a tree increased with DBH, CL, and CR, but decreased with greater CLSA (Table 6). Comparison of a tree with severe SNC (CLSA = 7.5) to a tree of the same DBH and crown size but with relatively mild SNC (CLSA = 5.5) suggested that SNC has reduced total branchwood surface area by an average of 7.4%.

The vertical distribution of branchwood surface area was related to tree size (DBH, HT), crown size (CL, CR), stand structure (TOPHT, RD), site quality (SI), and SNC severity (CLSA; Table 6). Although the beta parameters varied significantly by CLSA, the overall change in the vertical distribution of branchwood surface area across the full range in CLSA was not at all striking. Likewise, the distribution modes for total, primary branch axis, and lateral shoot surface area were remarkably similar (Fig. 1). Lateral (second order and higher) shoot surface area was slightly more evenly distributed than surface area of primary branch axes.

Stand-level

Wood area index (WAI; total surface area per unit ground area) ranged from 0.9 to 5.5, averaging 1.92 ± 0.89 (Fig. 2). Stem surface area comprised $54 \pm 13\%$ of the total WAI. BAI and SAI were positively correlated, but the relationship was sufficiently variable that the correlation was only marginally significant ($p = 0.10$). BAI declined with increasing stand age, and SAI increased with increasing stand density ($\mathrm{RD}_{\mathrm{DF}}$; Table 6). For a stand of given age,

Table 5 Specific shoot area (cm^2 g^{-1}) for five age classes of lateral shoots on Douglas-fir sample branches ($n = 309$)

Attribute	Mean	Standard deviation	Minimum	Maximum
1-year-old age class	2.67	1.57	0.36	7.36
2-year-old age class	3.08	1.56	1.39	9.55
3-year-old age class	2.53	1.08	1.15	7.07
4-year-old age class	2.21	0.97	1.12	6.08
≥ 5-year-old age class	1.92	0.78	0.95	5.01

Table 6 Model form, parameter estimates, R^2 and root mean square error (RMSE) for equations used in to estimate woody surface area in Douglas-fir plantations

Equation	Form	R^2	RMSE
(1) Specific shoot area (cm^2 g^{-1})	$\log(\text{SSA}) = 1.1075 + 0.4028 \times A_1 + 0.3389 \times A_2 + 0.1671 \times A_3 + 0.0427 \times \text{DIN\_CAN} - 0.0141 \times \text{BD} - 0.2467 \times \text{CL}$	0.26	0.28
(2) Primary branch taper	$\hat{d}_i = 0.2425 \times \text{BD}^{0.9554_1} \left(\frac{1-\sqrt{Z}}{1-\sqrt{0.2}}\right)^{\left(\begin{array}{l} -5.1210\times\sqrt{Z}+Z^{-0.2001}+1.6436\times\log(Z) \\ +1.4159\times\exp(Z)-0.0023\left(\frac{\text{BD}}{\text{BL}}\right)\end{array}\right)}$	0.91	3.45
(3) Individual branch surface area (cm^2)	$\text{BSA} = 7.1556 \times \text{BD}^{1.7278} \exp(-0.6643 \times \frac{\text{BHT}}{\text{HT}} + 0.0142 \times \text{SI})$	0.94	50.29
(4) Branchwood surface area of individual trees (m^2)	$\text{TPRISA} = \exp(1.1295 + 0.0348 \times \text{DBH} + 0.0163 \times \text{CL} + 0.9647 \times \text{CR} - 0.0352 \times \text{CLSA})$	0.69	7.35
	$\text{TLBSA} = \exp(0.3438 + 0.0252 \times \text{DBH} + 1.3759 \times \text{CR} - 0.0412 \times \text{CLSA})$		
	$\text{TBSA} = \exp(1.5136 + 0.0319\text{DBH} + 0.0124 \times \text{CL} + 1.0561 \times \text{CR} - 0.0372 \times \text{CLSA})$		
(5a) Beta parameters – total branchwood surface area	$a_{\text{BSA}} = 1.6895 - 0.0306 \times \text{CLSA} + 0.0001 \times \text{TPH} - 0.0175 \times \text{RD} + 0.0167 \times \text{SI}$	0.43	0.99
	$b_{\text{BSA}} = 0.6089 - 0.1670 \times \text{HT} + 0.1657 \times \text{HCM} + 0.1097 \times \text{CL} + 0.0232 \times \text{TOPHT}$		
(5b) Beta parameters – surface area of primary branch axes	$a_{\text{PRISA}} = 1.4892 + 0.0112 \times \text{HCM} - 0.0294 \times \text{CLSA} + 0.0212 \times \text{SI}$	0.47	0.98
	$b_{\text{PRISA}} = 0.0609 - 0.1644 \times \text{HT} + 0.1559 \times \text{HCM} + 0.1492 \times \text{CL} + 0.0342 \times \text{TOPHT}$		
(5c) Beta parameters – surface area of lateral shoots	$a_{\text{LBSA}} = 1.0071 - 0.0120 \times \text{DBH} + 0.5499 \times \frac{\text{DBH}}{\text{HT}} - 0.0293 \times \text{CLSA} + 0.9836 \times \text{CR}$	0.33	0.99
	$b_{\text{LBSA}} = 1.2325 - 0.1193 \times \text{HT} + 0.1252 \times \text{HCM} + 0.0579 \times \text{CL}$		
(6) Branchwood area and stem area indices	$\text{BAI} = \exp(-1.0043 - 0.0179 \times \text{AGE} + 0.0288 \times \text{TOPHT} + 0.2436 \times \text{FOLRET})$	0.68	0.32
	$\text{SAI} = \exp(-1.899 + 0.2629 \times \text{RD}_{\text{DF}} + 0.1346 \times \text{FOLRET})$		
(7) Tree area index	$\ln(\text{TAI}) = 0.7697 + 0.1055 \times \text{BA}_{\text{DF}} + 0.8389 \times \%\text{BA}_{\text{DF}} - 0.0169 \times \text{AGE} + 0.1449 \times \text{FOLRET}$	0.82	0.18

All parameter estimates are significant at $\alpha = 0.05$ level.

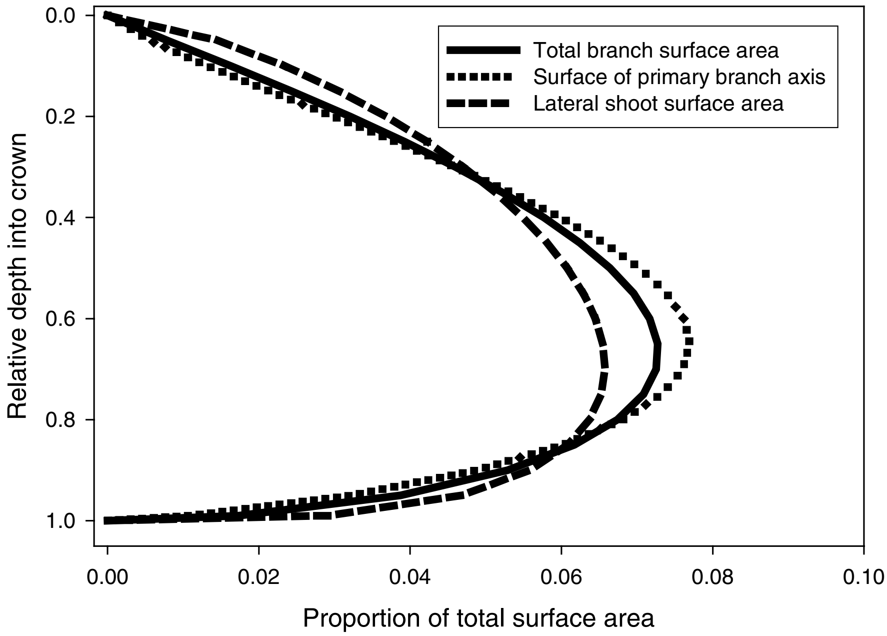
top height, and relative density, both BAI and SAI increased significantly with greater FOLRET (Table 6). Comparison of a stand with severe SNC (FOLRET = 1.5) to a relatively healthy stand (FOLRET = 3.5) implied that SNC reduced BAI and SAI by 34 and 24%, respectively (Fig. 3). At the stand level, wood surface area comprised 29 ± 12% of total tree surface (WAI as % of TAI). Overall, TAI showed a significantly positive relationship with RD_{DF}, $\%\text{BA}_{\text{DF}}$ and FOLRET, but decreased with age (Table 6, Fig. 4). The reduction in TAI due to SNC was approximately 25%.

Discussion

Previous studies of woody surface area have been based on relatively few samples and a very restricted geographic scope. In contrast, the Douglas-fir plantations sampled in this study covered a wide range in stand and site conditions that were representative of the northern half of the Oregon Coast Range. Although a high degree of natural variation in WAI was evident, a significant amount of this variation was accounted by site quality and stand structural attributes that are routinely manipulated by silvicultural treatment.

The series of models developed for scaling up to stand-level estimates of branchwood area confirm established allometric relationships between branch diameter and: branch woody mass (Maguire 1994; Baldwin et al. 1997), branch foliage mass (Xu and Harrington 1998; Kershaw and Maguire 1995; Baldwin et al. 1997), and branch foliage area (Kershaw and Maguire 1995). Branch position expressed as either depth into crown or relative crown height has a strong effect on Douglas-fir foliage mass or area, predominantly because the amount of foliage on a branch of given diameter declines near the base of the live crown as branches become increasingly suppressed and lose foliage. Although depth into crown emerges as influential in other species as

Fig. 1 Relative vertical distribution of surface area contributed by primary branch axes, lateral shoots, and their sum, as estimated from Eq. (5) for the average sampled Douglas-fir tree



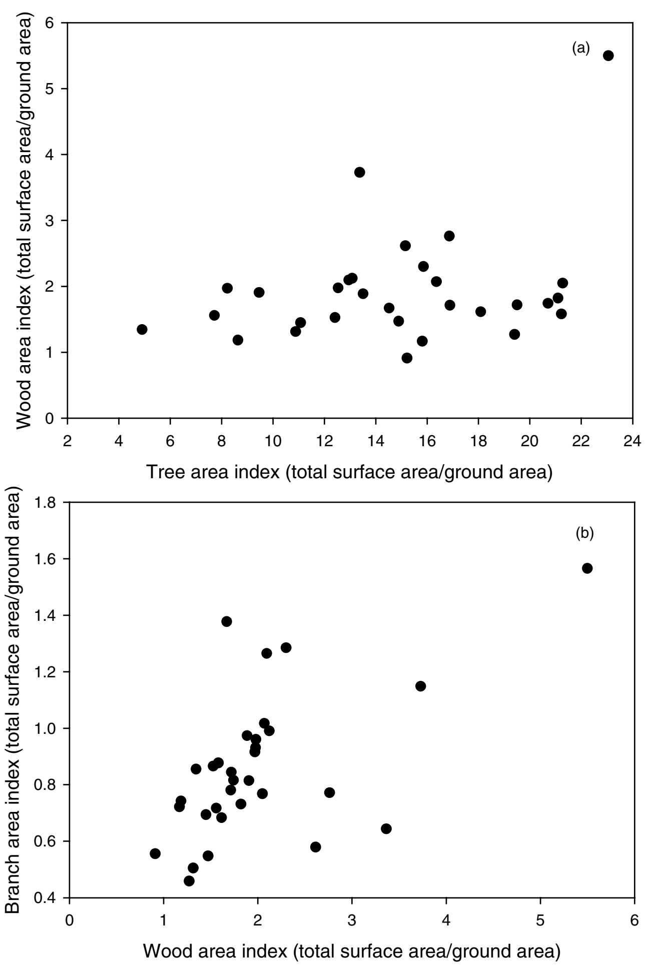


Fig. 2 Plots of (**a**) wood area index (WAI; woody surface area/ground area) over tree area index (TAI; total tree surface area/ground area) and (**b**) branchwood area index (BAI; total surface area/ground area) over WAI

well, it does not always imply this decline near crown base (Baldwin et al. 1997; Kenefic and Seymour 1999). As in this Douglas-fir study, however, Baldwin et al. (1997) found that much of the variation in woody surface area of loblolly pine branches could be accounted for by branch diameter and its depth into the crown.

Halldin (1985) found that, for a given height in the crown, lateral shoot and primary branch surface area were 5 and 13% of the needle area, remarkably close to the values of 4 and 14% for the Douglas-fir sample branches. Published values for specific shoot area (SSA) are uncommon; however, Mohren (1987) reported a fixed value of 0.3 m^2 kg^{-1} for the ratio of branch surface area to dry weight in Douglas-fir growing in the Netherlands. His value included both lateral shoots and the primary branch axes, so was not directly comparable to the mean SSA obtained in this study (2.44 cm^2 g^{-1} or 0.244 m^2 kg^{-1}). Furthermore, SSA was found to be highly variable within and between Douglas-fir trees in the Oregon Coast Range, so depending on the application, considerable advantage may be gained by accounting for this variation in SSA. Specific shoot area increased with increasing depth into crown for at least several reasons. First, the proportion of dead shoots increased with depth into crown and, because they are in various stages of decay, their mass was declining more quickly than their surface area. The results on vertical distribution of surface area also suggested that, through the bottom third of the crown, the proportion of total branchwood surface area contributed by primary branch axes (low surface area to mass ratio) declined while the contribution from lateral shoots (high surface area to mass ratio) increased (Fig. 1). Similarly, the decline in SSA with successively older age classes paralleled the increase in average

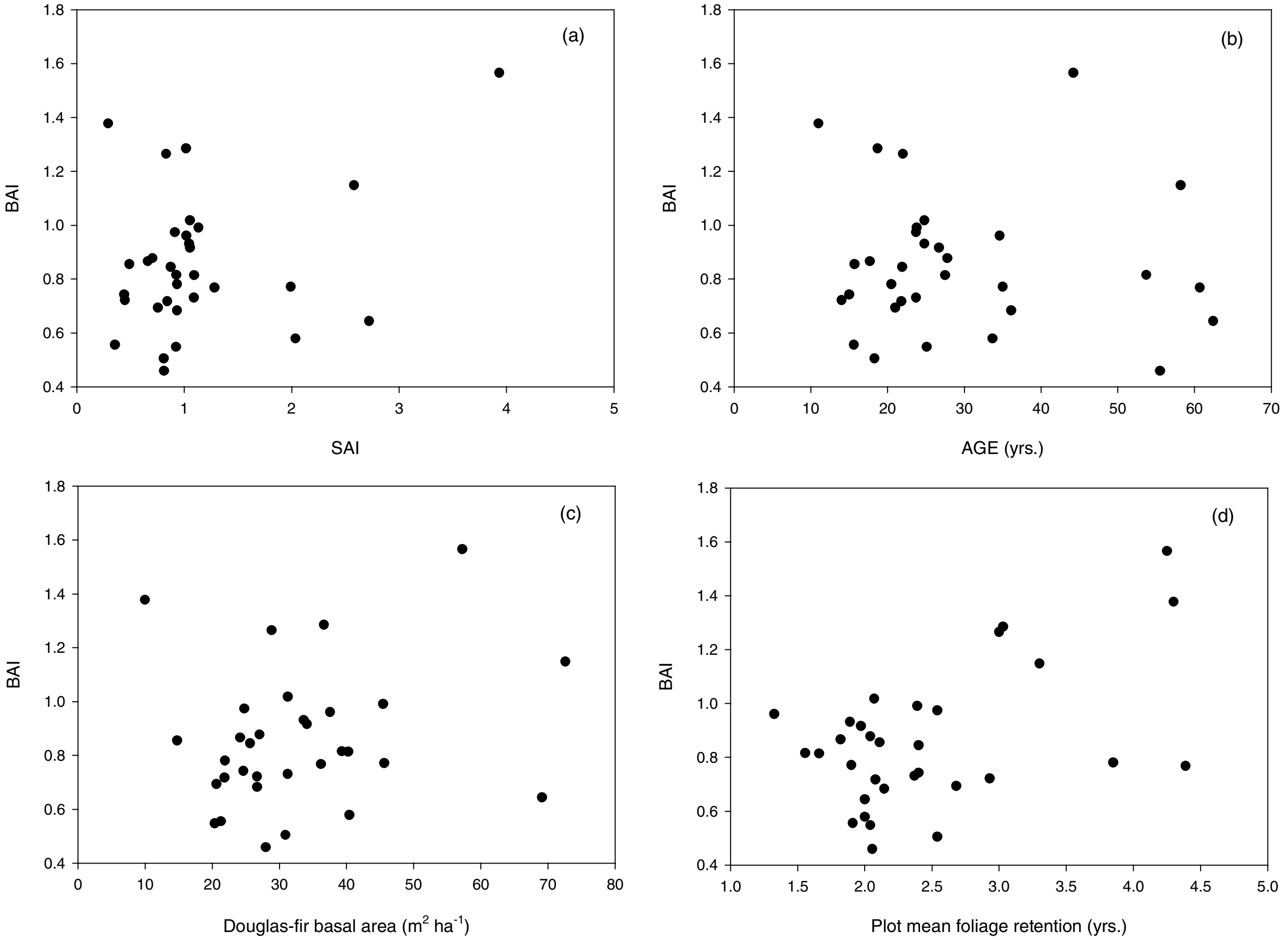


Fig. 3 Plots of branchwood area index (BAI; total surface area/ground area) over (**a**) stem area index (SAI; total surface area/ground area), (**b**) breast-height mean age, (**c**) Douglas-fir basal area ($m^2\ ha^{-1}$), and (**d**) plot mean foliage retention

shoot diameter and the decrease in surface area to mass ratio as shoots continue to grow. The effect of primary branch diameter is consistent with these patterns because an increase in this diameter would also imply a greater diameter and lower surface area to mass ratio in lateral shoots. Stem form in forest trees is strongly controlled by crown size and position (Larson 1965). The lack of any effect of foliated branch length on branch profile suggested that Douglas-fir branches are not analogs of Douglas-fir trees, at least across the range of conditions sampled in this study.

At the tree-level, total branchwood surface area was a function of tree size and several variables representing the size and vigor of the crown. This result differed only slightly from results presented by Baldwin et al. (1997) for loblolly pine (*Pinus taeda* L.); in that species, branchwood surface area was a function of DBH and CR (Baldwin et al. 1997). The dual importance of CL and CLSA in this study emphasized the significant impact of SNC on these Douglas-fir crowns. Weiskittel (2003) indicated that SNC reduced tree foliage area by 18%, while total branchwood was unaffected. In this analysis, the disease appears to have reduced tree

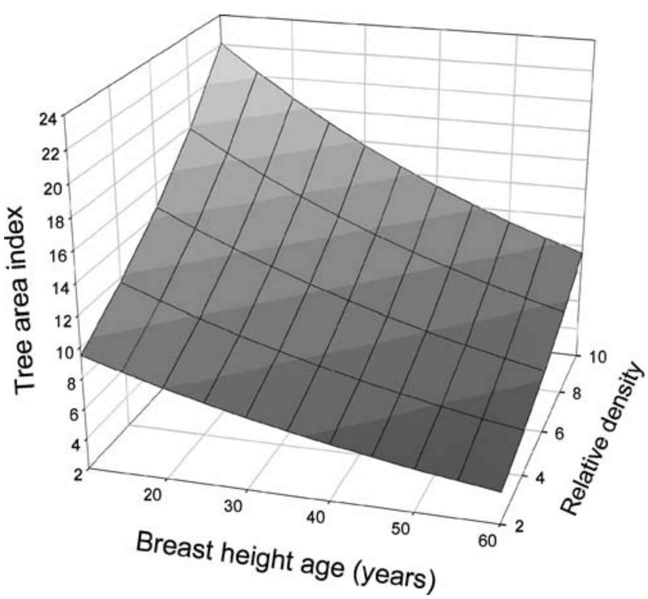


Fig. 4 Trend in tree area index (TAI) over breast height age and Douglas-fir relative density (Eq. (7)). Foliage retention (FOLRET) is set at 4 years and basal area in other species is assumed zero

branchwood surface area by nearly 8%, a change that may be related to the decline in branch size and reduction in number of secondary lateral shoots (Weiskittel 2003). Weiskittel et al. (2006) also found that the mode of vertical foliage distribution shifted significantly upward with increasing SNC. A similar trend was observed for branchwood surface area, but the relative change in the distribution was smaller than observed for foliage biomass. Baldwin et al. (1997) found that branchwood surface area tended to peak close to the crown midpoint, while the peak in this analysis was slightly lower in the crown. This is most likely a function of the differences in shade tolerance between the two species.

At the stand-level, values of WAI and the proportion of TAI that it accounts for have varied significantly, even for a single species (Bréda 2003). For example, Barclay et al. (2000) found WAI/TAI to be 41% in a 24-year-old Douglas-fir plantation, while Chen and Black (1991) report a WAI/TAI value of 8% for a similar Douglas-fir stand. In this study, WAI/TAI expressed as a percentage varied from 9 to 49% and showed a weak negative linear relationship with TAI. Increasing SNC severity also had a significantly positive effect on this proportion due to premature loss of foliage.

In the sampled Douglas-fir plantations, branches and main stem were nearly equal contributors of surface area to WAI ($12 \pm 3\%$ and $17 \pm 11\%$, respectively, of TAI). Smolander and Stenberg (1996) likewise indicated that branches and stem contributed approximately equal amounts (8 and 6%, respectively) to stand-level TAI. Total WAI varied in this study from 0.91 to 5.49, with the mean of 1.92 being very similar to that reported in Barclay et al. (2000). WAI in this study pertained to only live primary branches so inclusion of attached dead branches would raise the estimates slightly. Hagihara and Yamaji (1993), for example, found that dead branches comprised 5% of TAI in *Chamaecyparis obtusa*.

Tree area index (TAI) increased with Douglas-fir relative density because an increase in the latter implied fuller site occupancy due either to inherently higher carrying capacity of some sites or to a lighter thinning regime in some of the intensively managed stands. The decline in TAI with age was more surprising, but is consistent with some models of stand development that propose a slow decline in leaf area after a very early peak. If branchwood area parallels this trend, the decline with age is probably caused by the same mechanism, for example, crown separation caused by physical abrasion during wind sway (Rudnicki et al. 2003). In unmanaged stands, or stands managed at maximum stand density, the greater penetration of solar radiation and throughfall precipitation to the forest floor as the stand loses leaf and branchwood area is most likely a major cause of the shift from the stem exclusion stage of stand development to the understory re-initiation stage (Oliver and Larson 1996). The variation in interception of light and precipitation is even greater among stands managed at a wide range of stand densities. In these managed forests, therefore, a clearer understanding of canopy responses to silvicultural treatment, and corresponding insight into mechanisms by which these treatments influence forest productivity and ecosystem function, are key to achieving desired outcomes of management activities.

Conclusion

The procedure for deriving LAI from TAI is still a much debated question, largely because few direct measurements have been made to validate any generalizations. While stem and branches may be neglected in indirect estimates of LAI for fully leaved canopies, other corrections may be required for partially canopies defoliated by insects, disease, or pollution, or for species that retain a large number of dead branches on the lower stem (Kucharik et al. 1998). Douglas-fir plantations with severe SNC definitely meet both conditions, so direct estimates of woody surface area at the individual branch-, stem-, and stand-levels were the only way to account for the various sources of surface area reliably. SNC significantly reduced both branchwood and stem surface area at the tree- and stand-levels. Equations to predict branchwood surface area from easily measurable tree dimensions will help build an information base on stand surface area and its spatial distribution, as well as on changes brought about by natural stand dynamics and silvicultural treatments. These equations also provide reliable estimates of branchwood to needle surface area ratios in lieu of detailed and costly measurements from intensive study sites. Future progress in process-based modeling of Douglas-fir plantation growth, particularly in regions with varied stand health conditions or wide variation in silvicultural treatments and regimes, will require inclusion of WAI as a structural attribute because it has clear implications for numerous ecophysiological processes such as wood tissue respiration and absorption of solar radiation that would otherwise be available for photosynthetic tissues. Woody surface area also has important ecological functions, including service as a substrate for numerous canopy-dwelling organisms that contribute to forest biodiversity.

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