Application of the pipe model theory to predict canopy leaf area

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The pipe model theory presents the idea that a unit weight of tree foliage is serviced by a specific cross-sectional area of conducting sapwood in the crown. Below the crown, a large fraction of the tree bole may be nonconducting tissue, so the sapwood area would have to be known to estimate foliage. We applied the pipe model theory to the analysis of several western coniferous species to learn whether the distribution of canopy leaf area could be accurately estimated from knowledge of the sapwood cross-sectional area at various heights, including breast height (1.37 m). Results are excellent, but taper in the conducting area must be considered when sapwood area is measured below the crown.

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La théorie du modèle tubulaire introduit l'idée qu'une unité de poids du feuillage de la couronne d'un arbre est alimentée par une surface transversale spécifique d'aubier conducteur. Sous la couronne, une grande partie du tronc peut ne pas avoir de tissu conducteur, si bien que la zone d'aubier devrait être connue pour estimer le feuillage. Nous avons appliqué la théorie du modèle tubulaire à l'analyse de plusieurs espèces de conifères de l'Ouest pour savoir si la distribution de la surface de recouvrement foliaire pourrait être estimée avec précision en connaissant la surface transversale d'aubier à différentes hauteurs, y compris à hauteur de poitrine (1,37 m). Les résultats sont excellents, mais la conicité dans la zone conductrice doit être prise en considération lorsque la surface d'aubier est mesurée sous la couronne.

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Introduction

From an analysis of various vascular plants, Shinozaki *et al.* (1964a, 1964b) found that a linear proportionality exists between the weight of foliage and the weight of nonphotosynthetic tissue from the base of the live canopy upwards. They concluded that a given unit of leaves was serviced by a continuation of conducting tissue of constant cross-sectional area, analogous to a pipe system.

The original work by Shinozaki *et al.* (1964a) also clearly demonstrated that below the live crown no fixed ratio existed between total cross-sectional area and the supported foliage. They concluded that an increasing proportion of the vascular system in the stem below canopy height was nonconducting but did not quantify the relationship.

These ideas have been used to estimate the canopy leaf area from knowledge of the sapwood area at breast height (1.37 m), where diameter measurements are normally taken by foresters (Dixon 1971; Grier and Waring 1974; Waring *et al.* 1977; Whitehead 1978; Rogers and Hinckley 1979; Kaufmann and Troendle 1981). Initially, the analyses were expressed in foliage weight per unit of conducting area (Grier and Waring 1974).

Leaves of more shade-tolerant species, however, were known to vary in weight in proportion to light (Larcher 1980), so for general application of the pipe model, area was substituted for leaf weight.

Detailed studies of large trees, sectioned and delineated by conducting area at intervals below the crown (Huber 1928; Morikawa 1974), show that while the proportion of wood conducting water decreases toward the base, the area continues to increase. The absolute amount increases, particularly below the zone of butt swell. This would suggest that the pipe model should apply rigorously only when the conducting area is determined from the base of the crown upward. In the recent paper by Kaufmann and Troendle (1981), no differences were reported in the amount of leaf area supported by a unit of conducting sapwood tissue from breast height upward. In this paper we demonstrate that such differences do exist when trees are sampled that have an extensive part of their bole length free of branches. We further indicate that the cross-sectional area of sapwood tapers linearly between breast height and the base of the crown so that accurate estimates of canopy leaf area are possible from measurements of sapwood taken at breast height. Finally, we summarize for conifers all published accounts for the relationships between conducting sapwood area and leaf area.

TABLE 1. Sampled conifer species and their locations

| Taxa	Common name	n	Location in western Oregon
Abies amabilis (Dougl.) Forbes	Silver fir	4	44°10′ N, 122°20′ W
Abies grandis Lindl.	Grand fir	5	43°45′ N, 122°00′ W
Abies grandis × *concolor*	Hybrid fir	3	42°50′ N, 122°30′ W
Picea engelmannii (Parry) Engelm.	Englemann spruce	5	43°45′ N, 122°00′ W
Pinus contorta Laud. var. *murrayana* (Balf) Engel.	Lodgepole pine	8	43°30′ N, 122°00′ W
Pinus ponderosa Dougl.	Ponderosa pine	5	43°45′ N, 122°00′ W 42°20′ N, 123°00′ W
Pseudotsuga menziesii (Mirb.) Franco	Douglas-fir	5	42°20′ N, 123°00′ W
Sequoia sempervirens Endl.	Redwood	1	41°50′ N, 123°45′ W
Tsuga heterophylla (Raf.) Sarg.	Western hemlock	5	44°30′ N, 123°45′ W
Tsuga mertensiana (Bong.) Sarg.	Mountain hemlock	5	43°30′ N, 122°15′ W
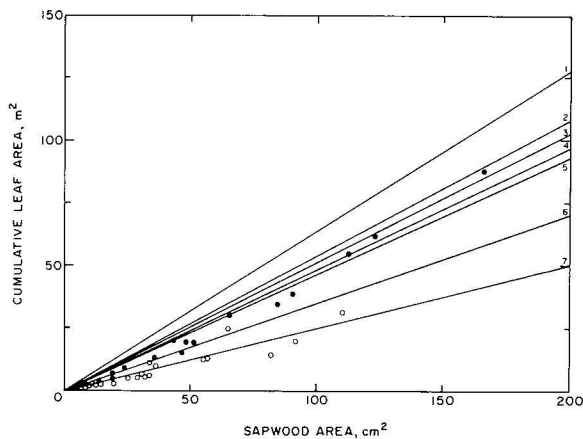
FIG. 1. The relationship between cumulative leaf area and sapwood area from quarter sections of the crown of eight taxa of western conifers. The regressions are fitted to 20 data points ($r^2 \geq 0.94$), except for redwood, fitted to four data points for a single tree. The *Abies grandis* × *concolor* hybrid had characteristics essentially the same as *Abies grandis*. 1, *Abies amabilis*; 2, *Pseudotsuga menziesii* (●); 3, *Sequoia sempervirens*; 4, *Abies grandis*; 5, *Tsuga heterophylla*; 6, *Picea engelmannii*; 7, *Pinus ponderosa* (○).
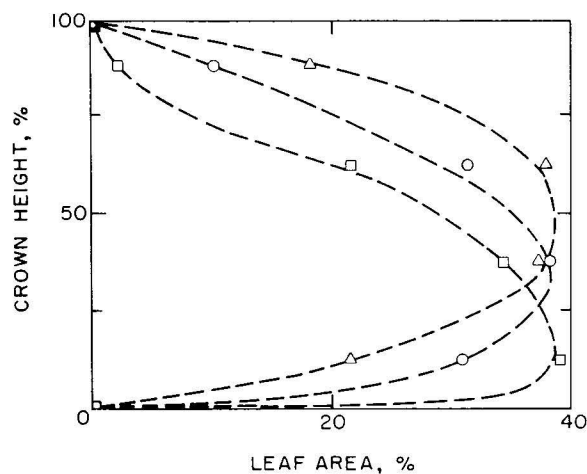

FIG. 2. The relative distribution of canopy leaf area from the base (○) to the top (100%) of the crown illustrate different patterns for *Pinus ponderosa* (△), *Pseudotsuga menziesii* (○), and *Abies grandis* (□). Data for each species represent the means of five trees. Except for the top quarter, other sections showed significant differences among species ($\alpha \leq 0.05$) with one-way analysis of variance.

Methods

Samples of taxa of western conifers were collected from a range of environments in western Oregon (Table 1). Except for redwood (*Sequoia sempervirens* Endl.) and hybrid fir (*Abies grandis* × *concolor* Lindl.), at least five trees of 5- to 25-cm diameter at breast height were analyzed for each species.

After each tree was cut near ground level, 1-cm-thick cross sections were cut at breast height and at 5-m intervals up to and including the base of the live crown. On smaller trees, the base of the crown often extended to breast height. The crown was divided into four equal lengths, from which cross sections were cut at the lower end. If the sapwood–heartwood boundary was clearly visible, it was immediately marked, and the tree sections were transported to the laboratory in a plastic bag.

Five branches were also randomly selected from each quarter section of crown and stored in plastic bags for later laboratory analysis. The remaining twigs with live foliage were clipped from each quarter and weighed in the field on a hanging scale to the nearest 0.1 kg.

In the laboratory, the 20 branches from each tree were stored not more than 1 week in a 3°C cold room before processing. All twigs were clipped from each branch and weighed with the needles; the needles were removed, reweighed, and dried at 70°C for 48 h. After drying, the needles were weighed again.

The surface area of a small subsample of fresh foliage from each branch was determined with a Li-Cor area meter (model
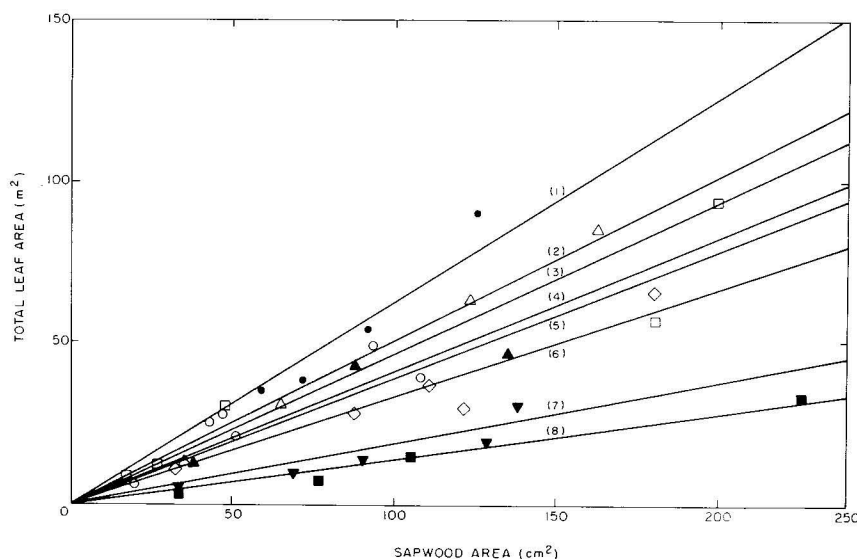
FIG. 3. The relationship between total canopy leaf area and sapwood area at diameter at breast height (1.37 m). The regression line for *Tsuga mertensiana* was not drawn because it overlaps that of *Pinus contorta* (slope coefficients 0.16 and 0.15, respectively). The samples were taken from only three to five trees for each species but r^2 values were $\geq$ 0.95. 1, *Abies amabilis* (●): 2. *Abies grandis* (△): 3. *Pseudotsuga menziesii* (○): 4. *Tsuga heterophylla* (□): 5. *Abies grandis* × *concolor* (▲): 6. *Picea engelmannii* (◇): 7. *Pinus ponderosa* (▼): 8. *Pinus contorta* (■). One tree initially identified as *A. amabilis* turned out to be *A. grandis*, reducing the sample to four for the first regression.

No. LI-3300). Subsamples were then dried and weighed. Area was determined on fresh foliage because foliage may shrink as much as 25% in drying.

The projected leaf surface area of each quarter section of crown was calculated by multiplying twig fresh weight by: (*i*) the ratio between the fresh weight of needles and the total fresh weight of the twig, (*ii*) the ratio of needle dry weight to needle fresh weight, and (*iii*) the ratio of fresh leaf area to needle dry weight. Total leaf area from each tree was determined by summing the quarter-section areas of the crown.

Sapwood area was determined on stem cross sections after carefully identifying the heartwood boundary. If the boundary was indistinct, the section was soaked in water, surface-dried a few minutes in an oven, then held in front of a strong light so that the translucent, conducting portion could be distinguished from the opaque nonconducting heartwood. The sapwood–heartwood boundary of each section was outlined and photocopied. Surface area of the photocopies of the sapwood rings were determined with the Li-Cor area meter to the nearest 0.1 cm^2.

Results

In our first analysis, cumulative leaf area from the top quarter section of each tree downward to the base of the crown was plotted against the related cross-sectional area of the sapwood. Linear relationships are illustrated in Fig. 1. *Tsuga mertensiana* and *Pinus contorta* were not measured for foliage distribution in the crown and thus are not included. Twenty data points, representing five trees and four sampling positions in each crown,

TABLE 2. Coefficients of leaf area : sapwood area (square metres per square centimetres) when sapwood is sampled at breast height (k_1) and at the base of the crown (k_2)

Taxa	k_1	k_2
Abies amabilis	0.63	0.64
Abies grandis	0.51	0.48
Abies grandis × *concolor*	0.40	0.48
Picea engelmannii	0.34	0.35
Pinus ponderosa	0.19	0.25*
Pseudotsuga menziesii	0.47	0.54
Tsuga heterophylla	0.41	0.46

*Regression coefficients differ significantly at the 5% level.

were used in developing linear regressions, all with $r^2 > 0.94$. We misidentified one *Abies amabilis* so for that species only four trees and 16 data points were available for the regression between sapwood area and leaf area.

These relationships may be transformed to provide an accurate picture of the vertical distribution of leaf area by plotting means of five trees, as shown for *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Abies grandis* in Fig. 2. Although the relative differences in foliage distribution in the crown may be representative of the species, variation within a given species can be expected because of competition from surrounding trees (Kohyama 1980).

TABLE 3. Ratios of projected leaf area to sapwood cross-sectional area
for selected conifers

Species	Leaf area : sapwood area, m^2/cm^2
Abies amabilis (Dougl.) Forbes	0.64[a]
Abies grandis Lindl.	0.48[a]
Abies lasiocarpa (Hook.) Nutt.	0.75[b]
Abies procera Rehd.	0.27*[c]
Juniperus occidentalis Hook.	0.18[d]
Picea engelmannii (Parry) Engelm.	0.35[a], 0.29[b]
Picea sitchensis (Bong.) Carr.	0.45[e]
Pinus contorta Engelm.	0.15*[a], 0.18[b], 0.17*[c]
Pinus nigra var. *maritima* (Ait.) Melv.	0.15*[f]
Pinus ponderosa Dougl.	0.25[a]
Pinus sylvestris L.	0.14*[g]
Pseudotsuga menziesii (Mirb.) Franco	0.54[a]
Tsuga heterophylla (Raf.) Sarg.	0.46[a]
Tsuga mertensiana (Bong.) Sarg.	0.16[a]

*Regression coefficients differ significantly at the 5% level and determined only at 1.37 m
above ground level rather than at base of crown.
[a]This paper.
[b]Kaufmann and Troendle (1981), converted to projected area by dividing by 2.5.
[c]Grier and Waring (1974), converted from biomass to leaf area in Waring *et al.* (1981).
[d]Gholz (1980).
[e]Whitehead (1981).
[f]J. M. Roberts, unpublished data. Institute of Hydrology. Wellingford, England.
[g]Whitehead (1978).

We also present linear regressions between sapwood cross-sectional areas measured at breast height and total leaf areas for three to five trees of each of eight species (Fig. 3). All regressions had r^2 values ≥0.95 but variation was much greater than around the regressions of crown sapwood area with cumulative leaf area in Fig. 1.

Table 2 compares coefficients of leaf area : sapwood area for those species sampled at breast height and at the base of the crown. Because the trees sampled were relatively small, the slope coefficients for the two regressions differed significantly only for *Pinus ponderosa*, by about 25%. The other species, however, also showed changes in sapwood area from the base of the crown to breast height ranging from 17 to less than 5%. In the latter cases, there was little distance between breast height and the base of the crown. These differences, even though not statistically significant, could account for much of the variation noted around individual regression lines presented in Fig. 3 because the trees sampled had differing fractions of their bole length in live crown.

Discussion

Results of this study suggest that the pipe model can be applied for predicting the amount and distribution of canopy leaf area for coniferous species. From the base of the crown upward, the sapwood area does indeed bear a constant relationship with a supported leaf area. Sapwood area taken at breast height may also relate well to total canopy leaf area, but these constants can be expected to vary with the ratio of bole to live crown (Albrektson 1980). Whitehead (1978) reported that Scots pine grown at different spacings had live crown lengths varying from 30% to more than 50% of tree height. However, he found good linear correlations between sapwood area at breast height and sapwood area at given points upward to the base of the crown (unpublished data, Dr. David Whitehead, Forest Research Institute, Roturua, New Zealand). The drawings of sapwood thickness of stems of individual trees in a report by Morikawa (1974) show that linear correlations should not extend much below breast height, particularly below butt swell.

Our sample trees were fairly small, like those of Kaufmann and Troendle (1981), with many having live crowns down to near breast height. Because of this, we suspected that differences between crown and breast-height coefficients (Table 2) were far larger on trees with extensive, clear boles. We support this contention by observing that on 21 ponderosa pines averaging 18 m in height and with live-crown ratios between 47 and 62, we found an average decrease of 42% in sapwood cross-sectional area between breast height and the base of the crown.

More recently, we calculated the decrease in sap-

wood area from breast height to the base of the crown on 16 Douglas-fir trees averaging 24 m in height and with live-crown ratios of 48% (unpublished data, Dr. Walter Thies, United States Forestry Service Forestry Sciences Laboratory, Corvallis, OR). We discovered that the sapwood area decreased linearly an average of 36% between the points of reference where there were no live limbs. We therefore recommend that taper in sapwood area be reported where measurements of sapwood are taken below the live crown.

With this restriction in mind, we have assembled a summary of the known coefficients for coniferous species (Table 3). The reported range in coefficients is nearly fivefold, ranging from 0.15 m^2 leaf area cm^{-2} of sapwood for *Pinus nigra* to 0.75 m^2 leaf area cm^{-2} of sapwood for *Abies lasiocarpa*. Even within genera a difference may occur, such as the more than threefold range between *Abies procera* and *Abies lasiocarpa*. It may well be possible that similar variation occurs within widely distributed species. For example, when equations developed to predict foliar biomass are converted to area, *Pseudotsuga menziesii* from the Rocky Mountains has a coefficient of 0.34, west coast varieties 0.54 m^2 (Snell and Brown 1978).

In general, the larger coefficients are associated with taxa that grow in mild climates or that represent shade-tolerant advanced successionary species such as *Abies grandis* or *Abies amabilis*. Species adapted to full exposure or desiccating environments show progressively smaller coefficients.

Where accurate estimates of wood production per unit of leaf area are required (Waring *et al.* 1981; Waring and Pitman 1980; Waring 1982), the refinements reported in this paper may be usefully employed. Also, where models of photosynthesis or other canopy-exchange processes require detailed knowledge of distribution of foliage area, analysis of sapwood area through the sampled crowns of trees of different species or size classes may provide an adequate estimate.

Acknowledgments

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