



Comparison of Methods of Estimating Leaf-Area Index In Old-Growth Douglas-Fir

Author(s): J. D. Marshall and R. H. Waring

Source: *Ecology*, Vol. 67, No. 4 (Aug., 1986), pp. 975-979

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1939820>

Accessed: 15-07-2015 21:55 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

COMPARISON OF METHODS OF ESTIMATING LEAF-AREA INDEX IN OLD-GROWTH DOUGLAS-FIR¹

J. D. MARSHALL² AND R. H. WARING³

Department of Forest Science, College of Forestry, Oregon State University,
Corvallis, Oregon 97331 USA

Abstract. Leaf-area index (*LAI*, the projected total surface area of foliage per unit ground area) of an old-growth Douglas-fir stand in western Oregon was estimated from litterfall, light interception, sapwood cross-sectional area, and tree diameter. Estimates made by the first three techniques were similar, but the estimate based on tree diameter was twice as high as the others. For large trees with variable amounts of live crown, estimates of leaf area based on tree diameter appear to be inaccurate; therefore, the exceedingly high leaf-area indices previously reported for Douglas-fir forests are unreliable. Sapwood cross-sectional area varies in correspondence with the canopy area and therefore is a better estimator of leaf area on large trees. Maximum *LAI* estimates based on sapwood area are similar to those for other temperate coniferous forests.

Key words: allometric equations; leaf-area index; light interception; litterfall; Oregon; *Pseudotsuga menziesii*; sapwood cross-sectional area.

INTRODUCTION

Accurate leaf-area measurements are critical for estimating fluxes of carbon, solar energy, and water in forested ecosystems. Photosynthesis, transpiration, respiration, and light interception can be directly related to leaf area (Gholz et al. 1976, Jarvis and Leverenz 1983), and these processes underlie correlations between leaf-area index (*LAI*, the projected surface area of foliage per unit ground area) and productivity (Gholz 1982, Schroeder et al. 1982, Waring 1983). Area is preferred to biomass as a measure of leaf amount because leaf mass changes from top to bottom of the canopy (Lewandowska and Jarvis 1977, Nygren and Kellomäki 1983) and varies seasonally (Smith et al. 1981) and with leaf age (Pike et al. 1977).

Leaf area increases for at least 40 yr in Douglas-fir stands (Long and Turner 1975) and then tends to equilibrate at a value apparently determined by site water balance (Grier and Running 1977) and fertility (Waring et al. 1978). The equilibrium *LAI* is essentially independent of stand density (Whitehead 1978). Equilibrium values in excess of 20 have been reported for old-growth Douglas-fir stands in the Pacific Northwest (Waring et al. 1978). These values, which far exceed those for other temperate coniferous forests (Gholz et al. 1976, Grier and Running 1977, Waring et al. 1978, Jarvis and Leverenz 1983), suggest that old-growth Douglas-fir forests have an unusual photosynthetic capacity that could have important ramifications for all analyses of ecosystem function, including those of hydrologic budgets and carbon and nutrient cycles.

Correlations between leaf area and tree diameter have often been used to estimate *LAI* (Kira and Shidei 1967, Whittaker and Woodwell 1968, Gholz et al. 1976, Grier and Logan 1977, Waring et al. 1978); however, trees of large diameter differ greatly in the amount of foliage they carry (Grier and Waring 1974, Whitehead 1978). *LAI* is perhaps better estimated from the cross-sectional area of the sapwood (Grier and Waring 1974, Snell and Brown 1978, Whitehead 1978). Because sapwood conducts water to the foliage, sapwood area maintains a closer relationship with leaf area than does diameter, particularly as heartwood begins to make up a large proportion of the basal area (Grier and Waring 1974, Long et al. 1981). Moreover, the relationship between leaf area and sapwood area appears to be reasonably constant for a given species within a broad geographic region (Waring et al. 1982), provided that one compensates for taper of the sapwood from the base of the live crown to measurement height (Whitehead et al. 1984). In this study, we compared estimates of *LAI* made from sapwood area, diameter, light interception, and litterfall in an old-growth Douglas-fir stand.

METHODS

Measurements were made in a 450-yr-old Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) stand in the H. J. Andrews Experimental Forest in the western Cascade Mountains, 70 km east of Eugene, Oregon (44° N, 122° W). This stand, designated Reference Stand 2 in previous studies (Zobel et al. 1976), has a substantial component of western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) coming in under the dominant Douglas-fir (Table 1). Below the hemlock is a sparse understory composed mostly of evergreen shrubs. Zobel et al. (1976) classified the stand in the *Tsuga heterophylla*/*Rhododendron macrophyllum*/*Berberis nervosa* habitat type.

¹ Manuscript received 21 January 1985, revised and accepted 30 September 1985.

² Present address: Environmental Science Department, General Motors Research Laboratories, Warren, Michigan 48090-9055 USA.

³ Address reprint requests to R. H. Waring.

TABLE 1. Characteristics of the old-growth stand, dominated by Douglas-fir, for which techniques of leaf-area estimation were compared (data are means \pm 1 standard error; $n = 6$ measurements except where noted).

Species	Basal area (m ² /ha)	Sapwood area (m ² /ha)	Density (trees/ha)	Height (m)	Litterfall (g·m ⁻² ·yr ⁻¹)	Light attenuation (%)
Douglas-fir	66.7 \pm 2.7	7.3 \pm 0.9	62 \pm 4	61 \pm 2*
Western hemlock	24.0 \pm 3.6	11.8 \pm 1.8	262 \pm 71	29 \pm 2†
Total	90.7 \pm 5.3	19.1 \pm 2.4	324 \pm 73	49 \pm 4	184	95.7 \pm 0.4

* $n = 14$ trees.

† $n = 9$ trees.

We estimated LAI first from foliage litterfall, with the assumption that the forest is at equilibrium leaf area (Long and Turner 1975). Foliage litterfall estimates were based on data from six 1-m² litter traps (Long-term Ecological Research data set, Oregon State University, Corvallis, Oregon, USA). Monthly averages calculated and summed from July 1977 to December 1980 yielded a value of 184 g·m⁻²·yr⁻¹ for conifer needles.

We multiplied this value by the specific leaf area, 74 cm²/g (projected leaf area [determined with an optical planimeter] per gram dry mass). This average value for all age classes of Douglas-fir foliage represents a 14% mass loss in the oldest foliage (Gholz et al. 1976). Mass losses of such magnitude occur just before abscission, presumably because of translocation of carbohydrates and nutrients (Wells 1981). Data available for western hemlock show that it is similar in specific leaf area to Douglas-fir (Gholz et al. 1976); therefore, we used the specific leaf area obtained from Douglas-fir foliage to convert values for both Douglas-fir and western hemlock foliage litterfall to leaf area. Our calculations yielded an estimate of 1.36 m²/m² (area of annual conifer litterfall per unit ground area).

Rates of leaf-biomass turnover for old-growth Douglas-fir in the Andrews forest were corrected for age differences in specific leaf area in order to obtain an annual turnover rate (t) of 0.17 (Overton et al. 1973, Pike et al. 1977). LAI was then calculated as

$$LAI = \frac{\Delta LAI}{t}, \quad (1)$$

where ΔLAI = the projected surface area of annual foliage litterfall (area [in square metres] of leaf area per square metre of ground). Again, the calculations were made with Douglas-fir data. Leaf turnover rates for western hemlock do not differ greatly from those for Douglas-fir (Grier and Logan 1977), but some error may have been introduced by using the common rate.

A second estimate of LAI was based upon measurements of light interception and the Beer-Lambert law (Jarvis and Leverenz 1983). Light levels above and below the canopy were estimated with blueprint paper, the "ozalid" technique (Friend 1961). Light integrators were left at each corner of each of the six litter traps for ≈ 24 h. The blueprint paper was calibrated against a net radiometer ($r^2 = 0.99$).

If one assumes that foliage is randomly distributed in space and that leaf inclination angles are spherically distributed (Jarvis and Leverenz 1983), one can calculate LAI from an empirically determined light-extinction coefficient (k):

$$LAI = \frac{-\ln(Q_i/Q_0)}{k}, \quad (2)$$

where Q_i = irradiance below the canopy and Q_0 = irradiance above the canopy.

Ungs (1981) calculated the extinction coefficient 0.48 for Douglas-fir foliage. The distribution of the residuals about the regression line showed that the fit of the regression would be improved if the line was not forced to pass through 1.0 for $LAI =$ zero; with this improvement the estimated k value was 0.40. We used both k values in our analysis.

A third estimate of LAI was obtained from the sapwood cross-sectional area (SWA). We selected trees for measurement around each of the six litter traps by standard variable-plot sampling techniques, using a basal area factor of 16 m²·ha⁻¹·tree⁻¹ (Husch et al. 1972). (The basal area factor is the number of units of basal area per hectare represented by each tree on the plot.) Sapwood thickness was measured from increment-bore cores obtained 1.37 m above ground on the side of the tree facing the plot center. Diameter measurements were corrected for the very irregular bark thickness by multiplying by 0.90 for Douglas-fir or 0.94 for western hemlock (Dilworth 1970). SWA was then calculated:

$$SWA = \pi \left\{ \frac{(D \cdot b)^2}{4} - \frac{[(D \cdot b) - 2s]^2}{4} \right\}, \quad (3)$$

where SWA = the sapwood area (in square centimetres), D = diameter (in centimetres), b = the bark thickness correction (diameter measured inside bark/diameter measured outside bark), and s = sapwood thickness (in centimetres). To obtain LAI , we multiplied the SWA value by the ratio of leaf area to SWA : 0.47 m²/cm² for Douglas-fir or 0.41 m²/cm² for western hemlock (Waring et al. 1982).

In variable-plot sampling, each sampled tree represents a known number of other trees per hectare; therefore, the leaf area of an individual tree can be converted to leaf area per hectare. The conversion factor is calculated by dividing the basal area factor by the basal area of the individual tree. The sum of prod-

TABLE 2. Estimates of leaf-area index, the projected total leaf surface area per unit ground area (m^2/m^2), in a 450-yr-old Oregon stand dominated by Douglas-fir.

Estimation method	Leaf-area index (Mean \pm SE)	Predictor
Light interception	6.6 \pm 0.2	Light extinction coefficient = 0.48
	7.9 \pm 0.3	Light extinction coefficient = 0.40
Litterfall	8.0 \pm 0.6	Foliage turnover rate = 17%/yr
Sapwood area	8.3* \pm 1.0	Basal area factor† = 16 m^2/ha
Diameter	16.2‡ \pm 2.5	Basal area factor = 16 m^2/ha

* Western hemlock foliage was estimated to make up 57% (SE = 4%) of the leaf area.

† The basal area per hectare represented by each tree on a plot

‡ Western hemlock foliage made up 47% (SE = 3%) of the leaf area.

ucts of this conversion factor and the leaf area of each sampled tree in a plot is the estimated leaf area per hectare, or *LAI*:

$$LAI = \sum_i \left(\frac{BAF}{BA_i} \cdot \frac{LA_i}{10,000 \text{ m}^2/\text{ha}} \right), \quad (4)$$

where *BAF* = the basal area factor, *BA_i* = basal area of tree *i* (in square metres), and *LA_i* = leaf area of tree *i* (in square metres).

A fourth estimate of *LAI* was obtained from tree diameter measurements and from the leaf biomass regressions of Gholz et al. (1979) corrected for specific leaf area of the species (Gholz et al. 1976). We expanded these values to a per-hectare basis using Eq. 4.

RESULTS AND DISCUSSION

The light-interception method with Ungs' (1981) extinction coefficient 0.48 gave a much lower estimate of *LAI* than the other methods. However, when the regression of his data was not forced through an intercept of 1.0 and the extinction coefficient 0.40 was calculated, the estimate was similar to those calculated from litterfall and sapwood area (Table 2). It is not clear why Ungs' data did not yield a regression line with an intercept of 1.0, although extinction coefficients can vary with sun angle (Jarvis and Leverenz 1983), leaf orientation (Kira et al. 1969), and the amount of branch and stem tissue (Swank and Schreuder 1974). In any case, measurement of light interception provides a reasonable estimate of *LAI* and merits further use because it is simple, inexpensive, and sensitive at low levels of light. It can certainly serve as a cross-check method for estimates of *LAI* made with other techniques.

The *LAI* estimate based on sapwood area was essentially the same as those derived from light extinction and litterfall. We expected somewhat higher estimates, as we made no correction for the difference in sapwood area at breast height and at the base of each tree crown (Waring et al. 1982, Whitehead et al. 1984). Albrektson (1984) and Espinosa (1985) have suggested various means of adjusting estimates of *LAI* made from sapwood measurements to compensate for differences in growth rates and for the highly variable sampling height.

The *LAI* estimate based on diameter measurements was about twice as high as the others. A similar value of 16.7 was independently estimated for the same stand from the same equation (Waring et al. 1978). We think allometric equations substantially overestimate leaf area on large trees because they are derived from samples of many smaller trees and a few trees having exceptional amounts of foliage. Although a more representative sample might improve the general relationship between diameter and leaf area, errors in estimates on large trees would still be high (Grier and Waring 1974, Long et al. 1981). In our sample, sapwood area in Douglas-fir trees >100 cm in diameter ranged from 5 to 22% of the total basal area at 1.37 m, and sapwood in western hemlock trees ranged from 34 to 67%. Diameter of small trees with little heartwood or of trees in very uniform stands may be used to predict leaf area just as well or slightly better than core samples of sapwood (Snell and Brown 1978). However, in stands that have a high proportion of heartwood, or in variable stands, sapwood area will provide a more accurate estimate of *LAI*.

The leaf-area indices reported for the coniferous forests of the Pacific Northwest are among the highest in the world (Gholz et al. 1976, Grier and Running 1977, Waring et al. 1978, Jarvis and Leverenz 1983). In every case, however, the high estimates have been based on diameter measurements (Table 3). Published estimates based entirely on sapwood area are uniformly lower, and as yet do not exceed 12.0. If light penetration is considered, it is difficult to see how *LAI* could much exceed 12.0. Even with the rather low light-extinction coefficient 0.40, 12 layers of leaves would reduce light at the bottom of the canopy to 0.8% of that above the canopy. This would, on the average, reduce net photosynthesis to zero (Krueger and Ruth 1969, Leverenz 1981). An index of 20.0 would reduce light levels to 0.03% of the value above the canopy. Foliage in the lower canopy would likely not survive under such conditions (Schulze et al. 1977). We believe that the extraordinarily high indices previously reported for the coniferous forests of the Pacific Northwest should be revised downward and brought more into line with those of other temperate-zone coniferous forests throughout the world.

TABLE 3. Published estimates of the maximum leaf-area index derived from measurements of sapwood area and diameter in Pacific Northwest forests dominated by Douglas-fir.

Leaf-area index	Age (yr)	Basal area (m ² /ha)	Stand density (trees/ha)	Location	Source
Estimated from sapwood area					
7.3	125	63	450	Cascade Range, Oregon	Waring et al. 1980
10.1	22	45	690	Coast Range, Oregon	Espinosa 1986
11.8	40	Puget Sound lowland, Washington	Keyes and Grier 1981
12.0	36	52	1980	Coast Range, Oregon	Waring et al. 1981
11.2	120	72	...	Cascade Range, Oregon	D. Santantonio (Forest Research Institute, Rotorua, New Zealand), <i>personal communication</i>
Estimated from diameter					
9.3	120–200	72	1250	Cascade Range, Oregon	Gholz 1982
15.2	450	116–129	...	Cascade Range, Oregon	Franklin and Waring 1981
18.2	100–130	Cascade Range, Oregon	Grier and Running 1977
18.6	250–450	Cascade Range, Oregon	Gholz et al. 1976
19.9	120–200	111	1500	Coast Range, Oregon	Gholz 1982
21.8	450	99	...	Cascade Range, Oregon	Waring et al. 1978

Lower leaf-area indices in the old-growth forests of the Pacific Northwest have an important implication for ecosystem studies. Estimates of foliar nutrient pools and canopy interception of precipitation will be substantially lower. However, the most important effects will be on ecosystem carbon budgets. The canopies of these forests probably assimilate substantially less carbon than we previously thought. The effect on estimates of forest productivity is likely to be rather small, however, in that the layers of leaves at the bottom of the canopy were never assumed to contribute much carbon to the functioning of the tree. Their carbon-assimilation rates were expected to be low (Schulze et al. 1977) and to barely exceed their maintenance respiration requirements (Waring and Schlesinger 1985).

ACKNOWLEDGMENTS

This work was supported by National Science Foundation grant DEB 8112455 to Oregon State University. This is Paper 1969, Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

LITERATURE CITED

- Albrektson, A. 1984. Sapwood basal area and needle mass of Scots pine (*Pinus sylvestris* L.) trees in central Sweden. *Forestry (Oxford)* **57**:35–43.
- Dilworth, J. R. 1970. Log scaling and timber cruising. Oregon State University Book Stores, Corvallis, Oregon, USA.
- Espinosa, M. 1986. Growth and structure of three adjacent 22 year-old Douglas-fir stands in the Oregon Coast Range. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Franklin, J. F., and R. H. Waring. 1981. Distinctive features of the northwestern coniferous forest: development, structure, and function. Pages 59–86 in R. H. Waring, editor. *Forests: fresh perspectives from ecosystem analysis*. Oregon State University Press, Corvallis, Oregon, USA.
- Friend, D. T. C. 1961. A simple method for measuring integrated light values in the field. *Ecology* **42**:577–580.
- Gholz, H. L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology* **63**:469–481.
- Gholz, H. L., F. K. Fitz, and R. H. Waring. 1976. Leaf area differences associated with old-growth forest communities in the western Oregon Cascades. *Canadian Journal of Forest Research* **6**(1):49–57.
- Gholz, H. L., C. C. Grier, A. G. Campbell, and A. T. Brown. 1979. Equations and their use for estimating biomass and leaf area of Pacific Northwest plants. Oregon State University Forest Research Laboratory Research Paper **41**.
- Grier, C. C., and R. S. Logan. 1977. Old-growth *Pseudotsuga menziesii* (Mirb.) Franco communities of a western Oregon watershed: biomass distribution and production budgets. *Ecological Monographs* **47**:373–400.
- Grier, C. C., and S. W. Running. 1977. Leaf area of mature northwestern coniferous forests: relation to water balance. *Ecology* **58**:893–899.
- Grier, C. C., and R. H. Waring. 1974. Conifer foliage mass related to sapwood area. *Forest Science* **20**:205–206.
- Husch, B., C. I. Miller, and T. W. Beers. 1972. *Forest mensuration*. Ronald Press, New York, New York, USA.
- Jarvis, P. G., and J. W. Leverenz. 1983. Productivity of temperate, deciduous and evergreen forests. Pages 233–280 in O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, editors. *Ecosystem processes: mineral cycling, productivity, and man's influence*. Volume 12D in *Physiological plant ecology: new series*. Springer-Verlag, New York, New York, USA.
- Keyes, M. R., and C. C. Grier. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research* **11**:599–605.
- Kira, T., and T. Shidei. 1967. Primary production and turnover of organic matter in different ecosystems of the western Pacific. *Japanese Journal of Ecology* **17**:70–87.
- Kira, T., K. Shinozaki, and K. Hozumi. 1969. Structure of forest canopies as related to their primary productivity. *Plant and Cell Physiology* **10**:129–142.
- Krueger, K. W., and R. H. Ruth. 1969. Comparative photosynthesis of red alder, Douglas-fir, Sitka spruce, and western hemlock seedlings. *Canadian Journal of Botany* **47**:519–527.
- Leverenz, J. W. 1981. Photosynthesis and transpiration in large forest-grown Douglas-fir: diurnal variation. *Canadian Journal of Botany* **59**:349–356.
- Lewandowska, M., and P. G. Jarvis. 1977. Changes in chlorophyll and carotenoid content, specific leaf area and dry weight fraction in Sitka spruce, in response to shading and season. *New Phytologist* **79**:247–256.

- Long, J. N., F. W. Smith, and D. R. M. Scott. 1981. The role of Douglas-fir sapwood and heartwood in the mechanical and physiological support of crowns and development of stem form. *Canadian Journal of Forest Research* **11**:459–464.
- Long, J. N., and J. Turner. 1975. Above-ground biomass and understory and overstory in an age sequence of Douglas-fir stands. *Journal of Applied Ecology* **12**:179–188.
- Nygren, M., and S. Kellomäki. 1983. Effect of shading on leaf structure and photosynthesis in young birch, *Betula pendula* Roth. and *B. pubescens* Ehrh. *Forest Ecology and Management* **7**:119–132.
- Overton, W. S., D. P. Lavender, and R. K. Hermann. 1973. Estimation of biomass and nutrient capital in stands of old-growth Douglas-fir. Pages 89–103 in *Mensuration, growth and yield. IUFRO biomass studies, S4.01*. College of Life Sciences and Agriculture, University of Maine at Orono, Orono, Maine, USA.
- Pike, L. H., R. H. Rydell, and W. C. Denison. 1977. A 400-year-old Douglas-fir tree and its epiphytes: biomass, surface area, and their distributions. *Canadian Journal of Forest Research* **7**:680–699.
- Schroeder, P. E., B. McCandlish, R. H. Waring, and D. A. Perry. 1982. The relationship of maximum canopy leaf area to forest growth in eastern Washington. *Northwest Science* **56**:121–130.
- Schulze, E.-D., M. I. Fuchs, and M. Fuchs. 1977. Spacial distribution of photosynthetic capacity and performance in a montane spruce forest of northern Germany. I. Biomass distribution and daily CO₂ uptake in different crown layers. *Oecologia (Berlin)* **29**:43–61.
- Smith, R. B., R. H. Waring, and D. A. Perry. 1981. Interpreting foliar analyses from Douglas-fir as weight per unit of leaf area. *Canadian Journal of Forest Research* **11**:593–598.
- Snell, J. A. K., and J. K. Brown. 1978. Comparison of tree biomass estimators—DBH and sapwood area. *Forest Science* **24**:455–457.
- Swank, W. T., and H. T. Schreuder. 1974. Comparison of three methods of estimating surface area and biomass for a forest of young eastern white pine. *Forest Science* **20**:91–100.
- Ungs, M. J. 1981. Distribution of light within the crown of an open-grown Douglas-fir. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Waring, R. H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. *Advances in Ecological Research* **13**:327–354.
- Waring, R. H., W. H. Emmingham, H. L. Gholz, and C. C. Grier. 1978. Variation in maximum leaf area of coniferous forests and its ecological significance. *Forest Science* **24**:131–140.
- Waring, R. H., K. Newman, and J. Bell. 1981. Efficiency of tree crowns and stemwood production at different canopy leaf densities. *Forestry* **54**:129–137.
- Waring, R. H., and W. H. Schlesinger. 1985. *Forest ecosystems: concepts and management*. Academic Press, Orlando, Florida, USA.
- Waring, R. H., P. E. Schroeder, and R. Oren. 1982. Application of the pipe model theory to predict canopy leaf area. *Canadian Journal of Forest Research* **12**:556–560.
- Waring, R. H., W. G. Thies, and D. Muscato. 1980. Stem growth per unit of leaf area: a measure of tree vigor. *Forest Science* **26**:112–117.
- Wells, C. G. 1981. Methods of estimating foliar biomass. Pages 107–114 in J. J. Bufalini and R. R. Arnts, editors. *Emissions. Volume 1 in Atmospheric biogenic hydrocarbons*. Ann Arbor Science, Ann Arbor, Michigan, USA.
- Whitehead, D. 1978. The estimation of foliage area from sapwood basal area in Scots pine. *Forestry* **51**:35–47.
- Whitehead, D., W. R. N. Edwards, and P. G. Jarvis. 1984. Conducting sapwood area, foliage area, and permeability in mature *Picea sitchensis* and *Pinus contorta* trees. *Canadian Journal of Forest Research* **14**:940–947.
- Whittaker, R. H., and G. M. Woodwell. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. *Journal of Ecology* **56**:1–25.
- Zobel, D. B., W. A. McKee, G. M. Hawk, and C. T. Dyrness. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. *Ecological Monographs* **46**:135–156.