Paul E. Schroeder

Brooks McCandlish

Richard H. Waring

and

David A. Perry

Department of Forest Science
Oregon State University
Corvallis, Oregon 97331

The Relationship of Maximum Canopy Leaf Area to Forest Growth in Eastern Washington

Abstract

Because forests in eastern Washington often exhibit stocking levels significantly below those predicted by standard yield tables, a method was sought to better estimate potential forest-site productivity. Maximum canopy development, expressed as layers of leaves per unit of ground area, or Leaf Area Index (LAI), was more closely related to maximum current stemwood production than was site index alone or a combination of site index, basal area, and age; however, the relationship was not regionally independent. A ratio of annual stemwood production per unit of leaf area, derived from measurements of radial growth and sapwood thickness, was responsive to changes in canopy density within a particular forest but was not sufficiently sensitive to estimate maximum potential LAI.

Introduction

Site index, defined as the height of dominant trees at a particular age, is often chosen as an empirical measure of the productive capacity of a forest site. Potential wood production can be estimated from empirical yield tables for a specific site index. An inherent assumption for such tables is that all areas with the same site index have equal productivity and support the same number of trees per unit area at a comparable age. This assumption, however, becomes invalid if the canopy leaf area that can be maintained varies. In arid regions particularly, where each tree requires more space to fulfill its moisture requirements, the resulting forests have less than normal stocking (Wilkstrom and Hutchinson, 1971; MacLean and Bolsinger, 1973). Normal yield tables overestimate productivity in such situations to the extent that stocking is below that predicted.

An alternative approach to estimating productivity was examined in this study. We tested a general premise that canopy leaf area might be directly related to the productivity of mixed stands of conifers across regions (Madgwick and Olson, 1974; Albrektson et al., 1977; Gholz, 1979) by examining fully stocked stands which exhibit some recent mortality of suppressed trees.

The overall goal of our research—to develop a method to estimate potential forest-site productivity—comprised two specific objectives: (1) testing the hypothesis that a regionally independent relationship exists between Leaf Area Index (LAI), the foliage surface area per unit of ground area, and productivity; and (2) estimating the maximum possible LAI for a site by extrapolating to the point where wood production per unit of

leaf area approaches zero as the forest canopy closes (Waring et al., 1980; Waring et al., 1981).

Study Area

The study area encompassed nearly all forested lands in Washington state located east of the crest of the Cascade Mountains. Excluded was the northernmost segment of Umatilla National Forest extending into the extreme southeastern corner of the state, since a vegetation analysis with predictions of forest productivity had already been completed there (Hall, 1973; MacLean and Bolsinger, 1973).

A wide range of environments is encountered across the area. Forests range in elevation from 600 to over 1800 m. Mean annual precipitation is approximately 2500 mm at the crest of the Cascades, but only about 250 mm at the lower forest boundary; considerable snow accumulates near the crest with lesser amounts at lower elevation. Temperatures vary, and cold winters are common throughout the eastern part of the state. In general, the growing season is cool and moist at higher elevations and hotter and drier at lower elevations (Franklin and Dyrness, 1973). The interaction between regional climate and local topography leads to a great diversity of forest types and a range in productivity of from < 2 to > 18 m^3 of stemwood ha^{-1}yr^{-1}.

Procedures

Stands were selected on the basis of two criteria: full stocking and absence of disturbance. We examined suppressed understory trees to assure that some mortality, indicating full stocking, had occurred within the last decade and evaluated disturbance by inspecting for stumps, skid roads, and evidence of recent fire; in some cases, undisturbed stands were impossible to locate. In these instances, we estimated whether the disturbance had occurred far enough in the past to allow probable recovery of both the overstory and understory trees. Because our primary emphasis was to test the more general hypothesis across regions, an effort was made to distribute sample plots sparsely over the entire study area, thereby including representatives of the whole spectrum of topographic, climatic, and forest types.

Initially located from maps, where roads crossed major climatic zones, stands were surveyed along transects similar in aspect, elevation, and vegetation; four to six sample points per stand were established along each transect. Care was taken to avoid microsites such as seeps and rock outcrops. Trees were sampled at each point with a metric 7-factor wedge prism and their diameters at breast height (DBH) recorded. Sapwood thickness, used to estimate LAI, and radial stem-growth increment for the previous five years were determined from increment cores extracted at breast height from the uphill side of each tree; the last five-year increment was averaged to avoid distortions from anomalies in a single year's growth. For each stand, total height and age at breast height were recorded for a subsample selected either from a range of diameters or from dominant trees appropriate for site-index determination.

A number of thinned stands were sampled to provide a wider range of canopy leaf areas on individual sites than occurred naturally so that the change in wood production per unit of leaf area as the canopy closes could be examined.

Analysis

Cross-sectional sapwood area at breast height was calculated from sapwood thickness and DBH measurements; the sapwood was assumed to be symmetric. Although the analyses required to relate sapwood area directly to leaf area had not been completed for most species east of the Cascades (east side) at the time of this study, Brown (1978) had developed equations to estimate foliage biomass as a function of DBH for five coniferous species in the intermountain region (Table 1). For each of these species regressions were fitted by least squares to the model:

$$\ln (DBH) = b_0 + b_1 \ln (SA) \qquad (1)$$

where SA = sapwood area in square centimeters.

These regressions, transformed and corrected for bias as suggested by Baskerville (1972), were substituted in Brown's equations. Foliage biomass was converted to projected (one-sided) leaf area by multiplying by factors from Gholz et al. (1976), Anderson et al. (1978), and Smith (1980) (Table 1). Four other coniferous species were common on the plots but no sapwood relationships with foliage were avaiable. For these, foliage biomass was estimated directly from DBH and then converted to leaf area (Table 2). Recently we have found that linear relationships for all these species exist if sapwood area is measured at the base of the crown. The curvilinear nature of equations in Table 1 result from taper in sapwood between DBH and the crown (R. H. Waring, P. Schroeder, and R. Oren, unpublished manuscript, Oregon State Univ., Forest Res. Lab). LAI was

TABLE 1. Equations for estimating projected leaf area (LA) in square meters from cross-sectional sapwood area (SA) in square centimeters at DBH. Derived from Brown's (1978) foliage biomass equations and biomass-leaf area conversion factors from the indicated sources.

Species	Equation
Abies grandis (Dougl.) Lindl.[1]	$LA = 2.6195 \ SA^{0.9562}(1.5916 + 0.2289 \ SA^{0.5949})$
Larix occidentalis Nutt.[2]	$LA = \exp \ (-0.29223 + 1.0225 \ \ln SA - 0.2451 \ SA^{0.6092})$
Pinus contorta Dougl. ex Loud.[2]	$LA = 0.26253 \ SA - 0.716$
Pinus ponderosa Dougl. ex Loud.[3]	$LA = (-1.3082 + 1.002.1 \ SA - 0.02211 \ SA^{0.53046})$
Pseudotsuga menziesii (Mirb.) Franco[4]	$LA = 0.59325 \ SA + 3.738$

[1]Gholz et al. (1976).
[2]R. H. Waring, unpub. data.
[3]Anderson et al. (1978).
[4]Smith (1980).

TABLE 2. Equations for estimating projected leaf area (LA) in square meters from DBH (D) in centimeters. Derived from Brown's (1978) foliage biomass equations and biomass-leaf area conversion factors from the indicated sources.

Species	Equation
Abies lasiocarpa (Hook.) Nutt.[1]	$LA = [0.00823 \ D^2 - 9.407 + \ln \ (0.5966 - 0.01672 \ D)] \ 6$
Picea engelmannii Parry ex Engelm.[1]	$LA = \exp \ [-1.3438 + 1.7096 \ \ln D + \ln \ (0.5783 - 0.0128 \ D)] \ 6$
Thuja plicata Donn[2]	$LA = \exp \ [-1.4368 + 1.6389 \ \ln D + \ln \ (0.6174 - 0.00459 \ D)] \ 8$
Tsuga heterophylla Raf. Sarg.[2]	$LA = \exp \ [-1.7002 + 1.7502 \ \ln D + \ln \ (0.5474 - 0.01456 \ D)] \ 8$

[1]Assumed to be similar to *Abies grandis*.
[2] Gholz et al. (1976).

calculated as the sum of canopy leaf area per hectare divided by 10,000 to provide units of leaf area, in square meters, per square meter of ground area.

Total cubic stemwood volume was estimated from diameter and height with volume tables compiled by Myers and Edminster (1972), Farr and LaBau (1971), and Faurot (1977). To estimate unknown tree heights, data from stands in which heights were measured over a range of diameters were fitted by least squares to the regression:

$$\ln (H/H^*) = b \ln (D/D^*) \tag{2}$$

where H = height
D = DBH
H* = height of dominant trees
D* = DBH of dominant trees.

The coefficient, b, was estimated to be 0.63; the r^2 of the relationship is 0.99. Annual growth increments were estimated from current height, DBH, radial increment, and Daubenmire Habitat Type according to Stage's (1975) model.

The study area was stratified into three broad geographic zones recognized by Franklin and Dyrness (1973) (Fig. 1). After preliminary analysis, we subdivided their southern region (S) on the basis of forest types. In some places in this part of the state, the western hemlock (*Tsuga heterophylla*) zone west of the Cascades (west side) extends over the Cascade crest. The vegetation there is different from that occurring in the west-side western hemlock zone or in more typical east-side forests (Franklin and Dyrness 1973). Sample plots belonging to this forest type were identified by the presence of *Abies amabilis* (Dougl.) Forbes, *Abies procera* Rehd., *Pinus monticola*
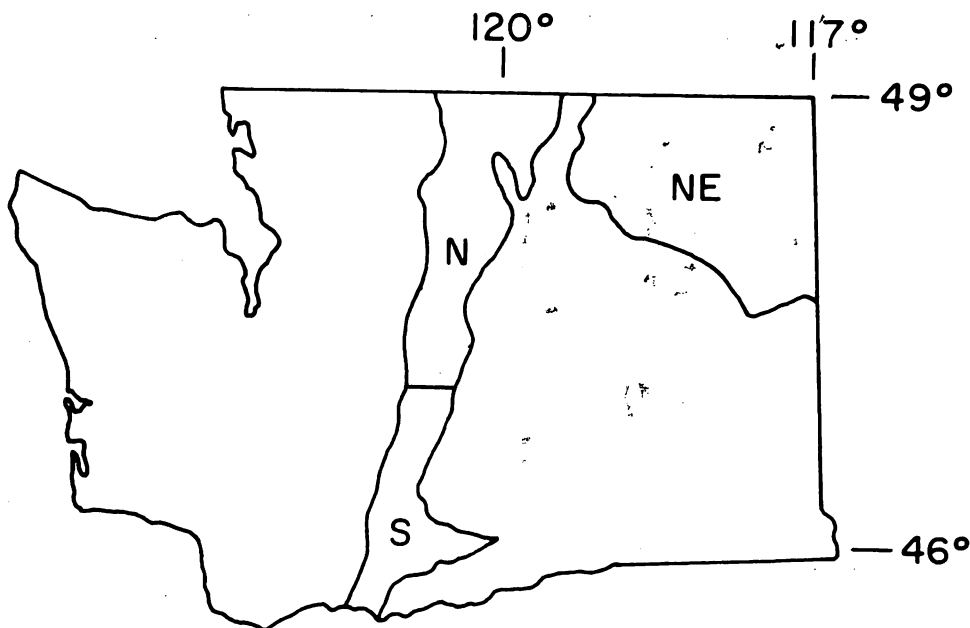

Figure 1. Geographic stratification of the study area into three broad vegetation zones. North (N), South (S), and Northeast (NE), based on Franklin and Dyrness (1973). The southern zone (S) was further subdivided into southwest (SW) and southeast (SE) vegetational zones which had irregular distributions within the broader zone but were easily distinguished on the basis of tree composition (see text for further explanation).
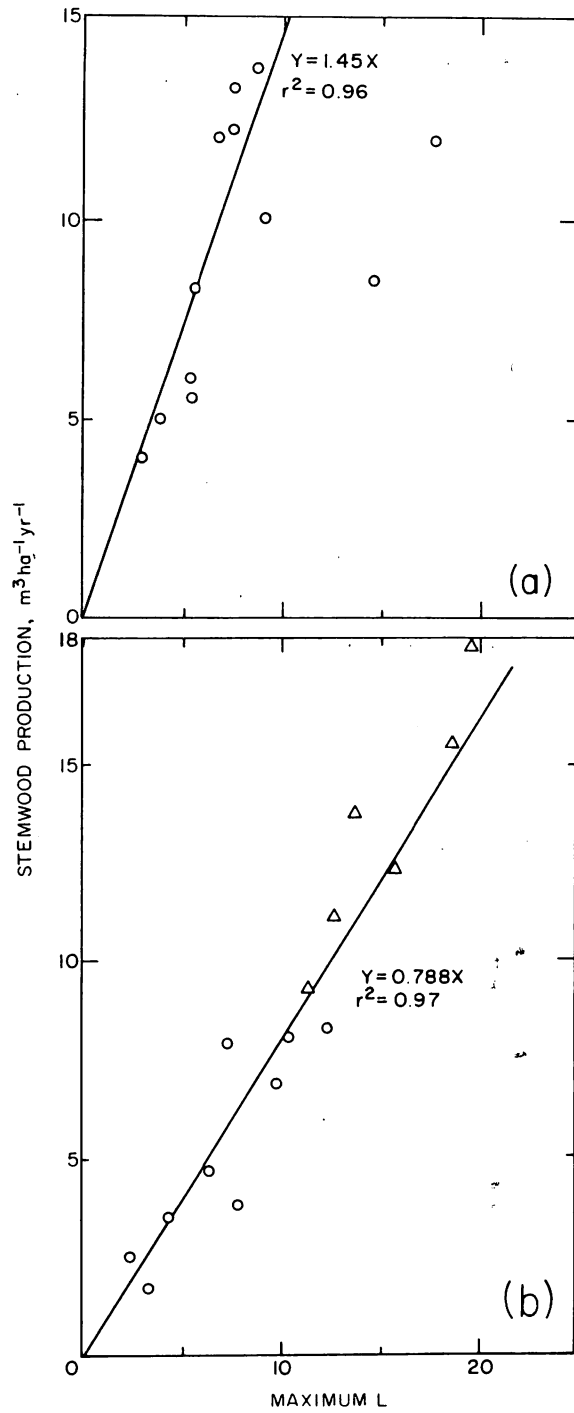
Figure 2. Relation of annual stemwood production to LAI for the study regions: (a) the NE and SE regions and (b) N and SW regions. Slopes of the regressions were significantly different, at the 5 percent level, for the two pooled data sets, a and b, up to an LAI of 10.

Canopy Leaf Area and Forest Growth in Eastern Washington   125

Dougl. ex D. Don, *Thuja plicata* Donn, or *Tsuga heterophylla* (Raf.) Sarg., and were grouped as the southern region, west-side type (SW); all other plots in this region were considered together as the east-side type (SE).

Results

The correlation between LAI and annual stemwood production calculated from average radial increment over the last five years was positive and significant at the five percent confidence level, but the relationship was not regionally independent (Fig. 2). Productivity increased in the NE and SE region at a rate of nearly 50 percent more than that observed for plots from N and SW regions, at least up to a LAI of 10. Two plots in the NE region fell below the linear predicted production. Both stands were of mixed composition and age with either a dense understory of slow growing *Abies grandis* and *Thuja plicata* or were over 225 years old. We suspect that natural or insect-induced mortality (Stoszek *et al.*, 1981) will soon occur and be followed by an increase in growth rate.

We correlated stemwood production with two other measures of productivity for a number of N and SW sites where Douglas-fir (*Pseudotsuga menziessi*) dominated fully stocked stands. First, site index alone was correlated with gross volume production; then a combination equation including site index, basal area, and age was used to predict yield after the procedures of Cochran (1979) (Fig. 3). Stemwood production was more closely related to LAI (Fig. 2b; $r^2 = 0.97$) than to either site index ($r^2 = 0.73$) or the combination equation ($r^2 = 0.91$).

From the field survey of variably stocked stands, sampling variation proved too great from only four to six points per stand to allow more than preliminary inferences
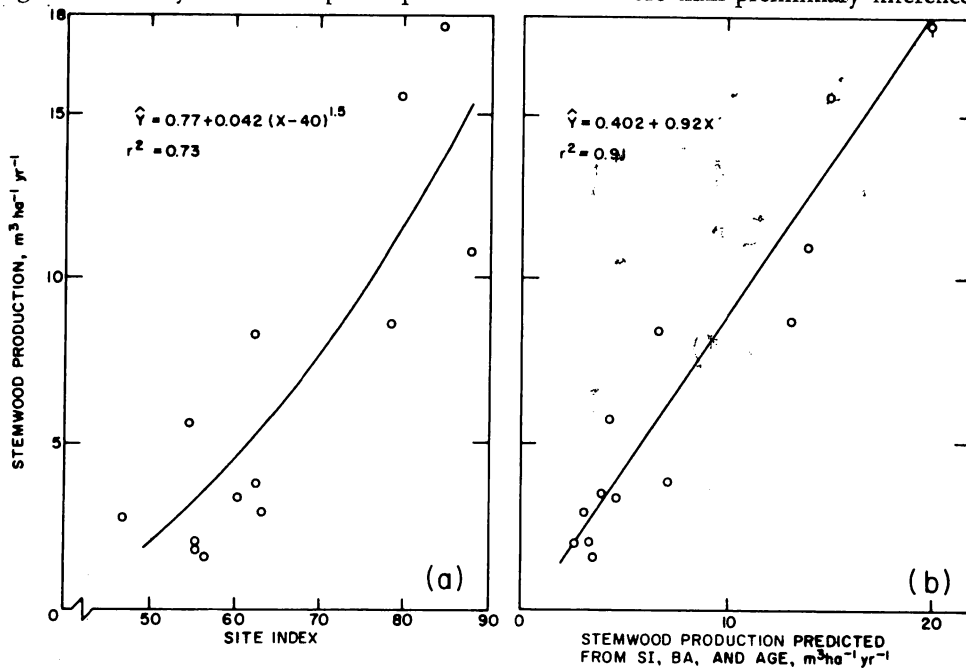

Figure 3. Relation of current stemwood production in 13 fully stocked stands in the N and SW regions to (a) site index and (b) productivity predicted by a combination equation including site index (SI), basal area (BA), and age.
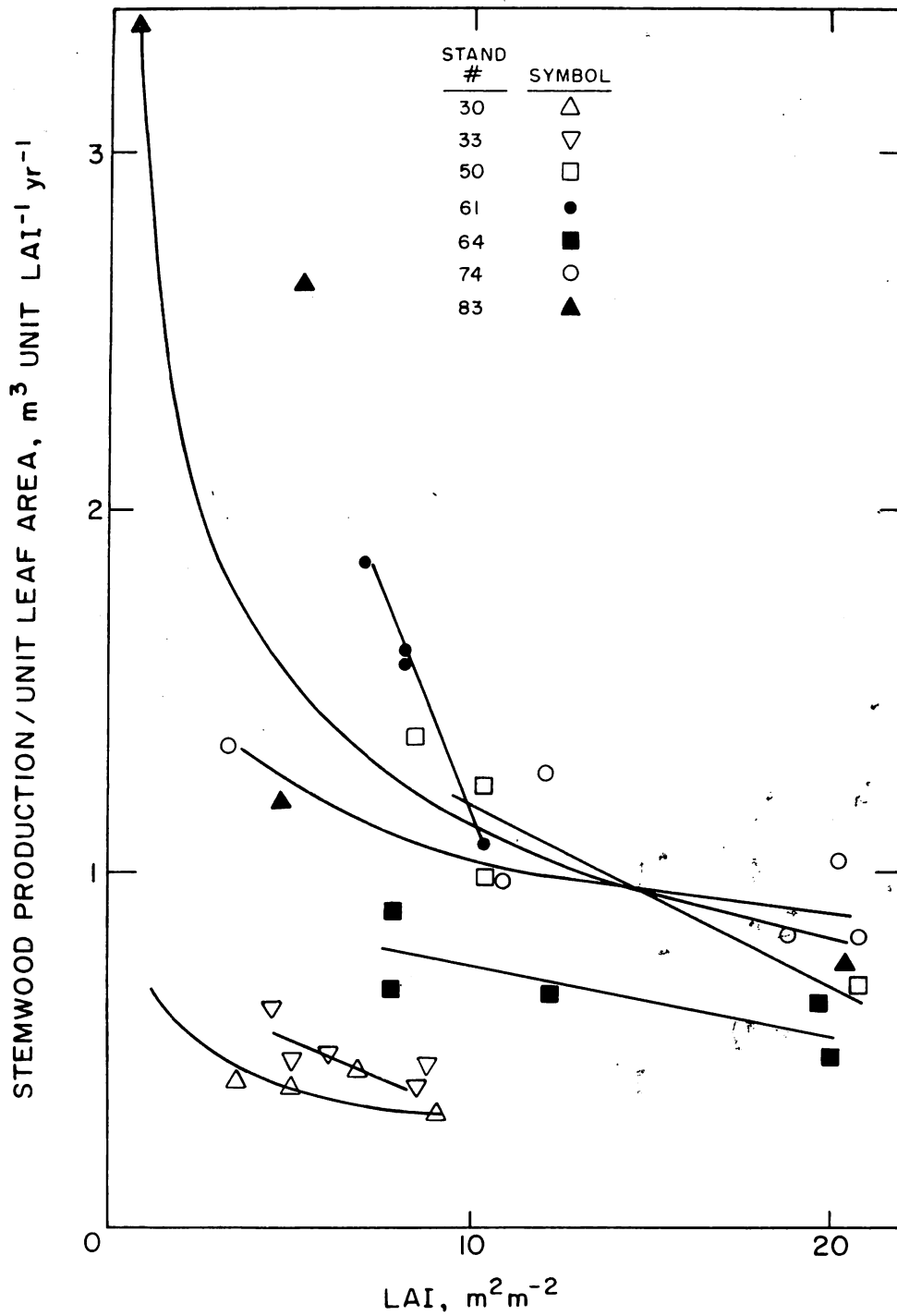
Figure 4. Relation of stemwood production per unit of leaf area to LAI. Lines represent data from seven distinct stands within which the stocking density of trees varied considerably.

about the relationship between estimated LAI and productivity on specific sites. In general, on a given site, net stemwood production per unit of leaf area decreased with increasing leaf area. In seven stands having a wide range in leaf area as a result of recent thinning, this relationship was significant at the 90 percent confidence level (Fig. 4). In undisturbed stands with high values of LAI, we noted that the crown on many trees became restricted to the upper bole. This constriction of the crown may promote more efficient capture of light and explain the small rate of decrease in growth efficiency at high leaf areas.

Discussion

More than two-fold differences in stemwood production by Douglas-fir stands with similar LAI have been reported previously (Waring et al., 1980). Such differences have been attributed to climatic variables that influence net carbon uptake (Waring et al., 1978). Another possibility is that total production may be similar, but that harsher edaphic environments stimulate a disproportionate allocation of carbohydrates into fine-root production (Keyes and Grier, 1981; Davidson, 1969). Because many trees are known not to produce annual growth rings under severe stress, wood production clearly is a relatively low priority compared with bud, shoot, and root growth (Gordon and Larson, 1968; Mooney, 1972; Rangnekar and Forward, 1973; Harris et al., 1978). A real difference also may occur in net photosynthesis per unit of leaf area (Emmingham and Waring, 1977) or in respiration of various tissues. Any combination of these factors could interact to cause substantial differences in wood production for a given canopy leaf area.

Although changes in growth efficiency followed an expected relationship with LAI, the relationship was too asymptotic to project the maximum LAI at which growth would approach zero. At a given LAI, where data from a range of stands overlapped, we did find a proportionality between wood production per unit of leaf area and stand productivity. For example, at a stand LAI of approximately 8.0 (Fig. 4), wood production per unit of leaf area varied from 0.4 to 0.8 to 1.4, whereas the equivalent stand yields were 2.8, 8.7, and 18 $m^3ha^{-1}yr^{-1}$. No doubt additional characteristics of the canopy, such as live crown ratio and relative distribution of foliage with height, also are important. We recognize that trees differing in height but with similar leaf area have significantly different respiration and intercept light differently. Thus, net assimilation of wood per unit of leaf area should differ correspondingly.

In comparing regions, we found it essential to know tree height to estimate stemwood-volume growth accurately. Stemwood growth estimated from regression of stemwood biomass on DBH alone, although appropriate for local conditions, was lower than that estimated from DBH and height data combined.

The most important practical result of the study is the recognition that maximum canopy leaf area is a superior estimator to conventional forestry measures employed on pure even-aged stands. The lower the maximum LAI, the more valid this conclusion.

Lloyd were especially helpful with preliminary planning for the field work and pro-vided valuable advice throughout the course of the investigation.

Literature Cited

Albrektson, A., A. Aronson, and C. O. Tamm. 1977. The effect of forest fertilization on primary. production and nutrient cycling in the forest ecosystems. Silva Fenn. 11:234-239.

Anderson, H. E., R. D. Schuette, and R. W. Mutch. 1978. Timelag and Equilibrium Moisture Content of Ponderosa Pine Needles. U.S. Dept. Agric., Forest Service, Res. Pap. INT-202, Ogden, Utah.

Baskerville, G. L. 1972. Use of logarithmic regressions in the estimation of plant biomass. Can. J. For. Res. 2:49-53.

Brown, J. K. 1978. Weight and Density of Crowns of Rocky Mountain Conifers. U.S. Dept. Agric., Forest Service, Res. Pap. INT-197, Ogden, Utah.

Cochran, P. H. 1979. Gross Yields for Even-aged Stands of Douglas-fir and White or Grand Fir East of the Cascades in Oregon and Washington. U.S. Dept. Agric., Forest Service, Res. Pap. PNW-263, Portland, Oregon.

Davidson, R. L. 1969. Effects of soil nutrients and moisture on root/shoot ratios in *Lolium perenne* L. and *Trifolium repens* L. Ann. Bot. 33:571-577.

Emmingham, W. H., and R. H. Waring. 1977. An index of photosynthesis for comparing forest sites in western Oregon. Can. J. For. Res. 7:165-174.

Farr, W. A., and V. J. LaBau. 1971. Volume Tables and Equations for Old-Growth Western Red Cedar and Alaska Cedar in Southeast Alaska. U.S. Dept. Agric., Forest Service, Res. Note PNW-167, Portland, Oregon.

Faurot, J. L. 1977. Estimating Merchantable Volume and Stem Residue in Four Timber Species: Ponderosa Pine, Lodgepole Pine, Western Larch, and Douglas-fir. U.S. Dept. Agric., Forest Service, Res. Pap. INT-196, Ogden, Utah.

Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. U.S. Dept. Agric., Forest Service, Gen. Tech. Rept. PNW-8, Portland, Oregon.

Gholz, H. L. 1979. Limits on Aboveground Net Primary Production, Leaf Area, and Biomass in Vegetational Zones of the Pacific Northwest. Oregon State Univ., Corvallis, Ph.D. thesis.

———, F. K. Fitz, and R. H. Waring. 1976. Leaf area differences associated with old-growth forest, communities in the western Oregon Cascades. Can. J. For. Res. 6:49-57.

Gordon, J. C., and P. R. Larson. 1968. Seasonal course of photosynthesis, respiration and distribution of ^{14}C in young *Pinus resinosa* trees as related to wood formation. Plant Physiol. 43: 1617-1624.

Hall, F. C. 1973. Plant Communities of the Blue Mountains in Eastern Oregon and Southeastern Washington. U.S. Dept. Agric., Forest Service, Pac. Northwest Reg. R6, Area Guide ß-1.

Harris, W. F., R. S. Kinerson, and N. T. Edwards. 1978. Comparison of belowground biomass of natural deciduous forests and loblolly pine plantations. Pedobiologia 17:369-381.

———, D. Santantonio, and D. McGinty. 1980. The dynamic belowground ecosystem, pp. 119-129 *in* R. H. Waring (ed.). Forests, Fresh Perspectives from Ecosystem Analysis. Proceedings 40th Annual Biology Coloquium. Oregon State Univ., Corvallis.

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. Can. J. For. Res. 11:599-605.

MacLean, C. D., and C. L. Bolsinger. 1973. Estimating Productivity on Sites with a Low Stocking Capacity. U.S. Dept. Agric., Forest Service, Res. Pap. PNW-152, Portland, Oregon.

Madgwick, H. A. I., and D. F. Olson. 1974. Leaf area index and volume growth in thinned stands of *Liriodendron tulipifera*. J. Appl. Ecol. 11:575-579.

Mooney, H. A. 1972. The carbon balance of plants. Annu. Rev. Ecol. & Systematics 3:315-345.

Myers, C. A., and C. B. Edminster. 1972. Volume Tables and Point Sampling Factors for Engelmann Spruce in Colorado and Wyoming. U.S. Dept. Agric., Forest Service, Res. Pap. RM-95, Ft. Collins, Colorado.

Rangnekar, O. V., and D. F. Forward. 1973. Foliar nutrition and wood growth in red pine: effects of darkening and defoliation on the distribution of ^{14}C-photosynthate in young trees. Can. J. Bot. 51:103-108.

Smith, R. H. 1980. Seasonal Variation in Leaf Weight and Nitrogen Content of Douglas-fir Plantations in the Coast Range and Cascade Mountains of Western Oregon. Oregon State Univ., Corvallis, M.S. thesis.

Stage, A. R. 1975. Prediction of Height Increment for Models of Forest Growth. U.S. Dept. Agric., Forest Service, Res. Pap. INT-164, Ogden, Utah.

Stoszek, K. J., P. G. Mika, J. A. Moore, and H. L. Osborne. 1981. Relationships of Douglas-fir tussock moth defoliation to site and stand characteristics in northern Idaho. For. Sci. 27: 431-448.

Waring, R. H., W. H. Emmingham, H. L. Gholz, and C. C. Grier. 1978. Variation in maximum leaf area of coniferous forests in Oregon and its ecological significance. For. Sci. 24:131-140.

————, K. Newman, and J. Bell. 1981. Efficiency of tree crowns and stemwood production at different canopy leaf densities. Forestry 54:15-23.

————, W. G. Thies, and D. Muscato. 1980. Stem growth per unit of leaf area: a measure of tree vigor. For. Sci. 26:112-117.

Wilkstrom, J. H., and S. B. Hutchinson. 1971. Stratification of Forest Land for Timber Management Planning on the Western National Forests. U.S. Dept. Agric., Forest Service, Res. Pap. INT-108, Ogden, Utah.