Leaf area differences associated with old-growth forest communities in the western Oregon Cascades[1]

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Total leaf area varied from 20 to 42 m^2/m^2 in 250- to 450-year-old forest communities developed under different temperature and moisture conditions. The largest values were in communities at midelevations where winter snowpack accumulated and growing-season temperatures were cool. Shrub and herb leaf area varied from 3% to 14% of the total. Equations for converting from foliage biomass to surface area are included for most species encountered.

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La surface foliaire totale variait de 20–42 m^2/m^2 dans des groupements forestiers âgés de 250–450 ans formés sous diverses conditions de température et d'humidité. Les valeurs les plus fortes ont été observées dans les peuplements situés à mi-élévation, où la neige s'accumule en hiver et où les températures de la saison de croissance sont fraîches. La surface foliaire des arbustes et des herbes variait de 3% à 4% de la surface foliaire totale. L'article fournit des équations de conversion de la biomasse de feuillage à la surface foliaire pour la plupart des espèces qui s'y rencontrent.

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Introduction

Leaf area and its spatial distribution is essential for estimating photosynthesis, transpiration, respiration, canopy interception, and energy transmission to the ground. Thus, it is a basic structural feature required in all terrestrial ecosystem studies.

This study had two major objectives: (1) to develop techniques enabling one to assess foliage areas for a wide variety of species characteristic of forest communities in the Cascade Mountains of western Oregon, and (2) to evaluate whether leaf area differences among major vegetational units are associated with measured moisture and temperature gradients.

Study Areas

The study was confined to the H. J. Andrews Experimental Forest, a 6000-ha watershed 60 km east of Eugene, Oregon (44° N, 122° W). Dyrness *et al.* (1974) recognized 23 mature forest communities there, and Zobel *et al.* (1974) described their ecological distributions in terms of measured gradients of plant moisture stress (Waring and Cleary 1967) and temperature (Cleary and Waring 1969) (Fig. 1). 'Reference stands' (RS) representing the major communities were established for detailed analysis (Zobel *et al.* 1974). To assess possible differences in leaf area, six reference stands representing a broad spectrum of environments were selected. Descriptions of these stands are given in Table 1 and their locations in environmental coordinates are designated in Fig. 1. In all stands 250- to 450-year-old Douglas fir (*Pseudotsuga menziesii* (Mirb) Franco var. *menziesii*) was the major overstory tree, constituting from 55 to 98% of the total tree foliage biomass.

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TABLE 1. Descriptions of six stands (RS) studied

RS	Community	Elevation, m	Description
1	*Pseudotsuga menziesii / Holodiscus discolor* (PSME/HODI)	490	Hot, dry; Douglas-fir climax
2	*Tsuga heterophylla / Rhododendron macrophyllum / Berberis nervosa* (TSHE/RHMA/BENE)	490	Modal; hemlock climax
4	*Abies amabilis / Tiarella unifolia* (ABAM/TIUN)	1310	Subalpine; silver-fir climax
5	*Tsuga heterophylla – Abies amabilis / Rhododendron macrophyllum / Berberis nervosa* (TSHE–ABAM/RHMA/BENE)	885	Midelevation; hemlock / silver-fir climax
6	*Tsuga heterophylla / Castanopsis chrysophylla* (TSHE/CACH)	610	Dry; hemlock climax
7	*Tsuga heterophylla / Polystichum munitum / Oxalis oregana* (TSHE/POMU/OXOR)	490	Very wet; hemlock climax

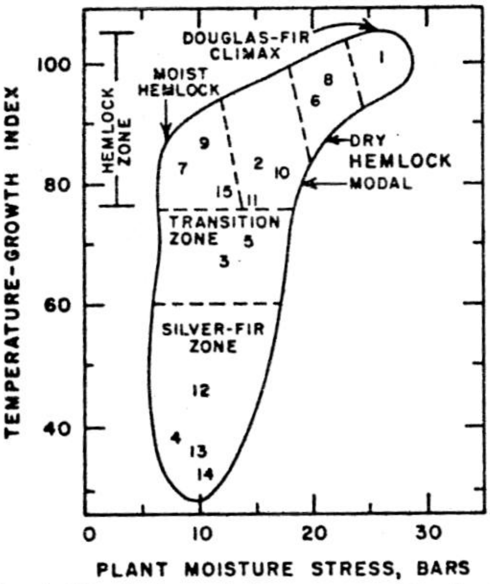

FIG. 1. Distribution of plant communities in the H. J. Andrews Experimental Forest (after Zobel *et al.* 1974). Moisture stress gradient represents predawn measurements when soil water reserves were minimal for the year. The temperature gradient is a physiological assessment of daily air and soil temperatures throughout the growing season for Douglas fir. Numbers refer to reference stands where detailed analysis of vegetation and environment were made.

TABLE 2. Regression equation constants for foliage biomass of major tree species[a]

Species	*A*	*B*	*R*²
P. menziesii	−3.890	1.890	0.88
T. heterophylla	−4.195	2.119	0.96
A. amabilis	−5.480	2.380	0.97
A. procera	−4.990	2.190	0.99
T. plicata	2.0997	1.915	0.99
C. chrysophylla	−3.0258	1.607	0.79

[a] All equations are of the form ln(dry foliage wt.) = A + B ln(DBH). Dry foliage wt. is in kilograms, DBH is in centimetres.

Methods

Estimating Foliar Biomass (see Tables 2 and 3)

Because most foliage data from coniferous forests are reported as biomass, one must first use mensurational techniques to estimate biomass and then convert to leaf area.

Grier (unpublished) furnished foliage biomass equations for Douglas fir, golden chinkapin (*Castanopsis chrysophylla* (Dougl.) A. DC.), and noble fir (*Abies procera* Rehd.). The equation for western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) was derived from a composite of data from Krumlik (1974) and Fujimori (1971). The equation for silver fir (***Abies amabilis*** (Dougl. Forbes) was derived from a composite of data from Krumlik (1974) and Grier (unpublished). Foliage biomass for western red cedar (***Thuja** plicata* Donn.) was calculated using a common logarithm equation for *Thuja occidentalis* L. (Reiners 1972). Foliage biomass for mountain hemlock (***Tsuga** mertensiana* (Bong.) Carr.), a minor overstory conifer, and Pacific yew (*Taxus brevifolia* Nutt.), a minor understory conifer, was estimated using the equation for western hemlock. For sugar pine (*Pinus lambertiana* Dougl.), foliage biomass was estimated from the Douglas fir equation.

For the seven most abundant shrubs, methods were sought that would allow rapid, objective, and accurate estimates of foliage biomass. Easily measurable inde-

TABLE 3. Understory foliage biomass equations

Species	Sample size	Equation[a]	R^2
Acer circinatum[b]	132	$X = 9.03(D^2L_{\max})^{\frac{1}{2}}$	0.90
Berberis nervosa	32	$X = 14.218+1.984(\%\text{cover})$	0.80
Rhododendron macrophyllum	40	$\ln(X) = 0.067177 + 0.60981 \ln(D^2L_{\max})$	0.90
Gaultheria shallon	32	$\ln(X) = 1.5137 + 0.70263 \ln(\%\text{cover})$	0.83
Xerophyllum tenax	22	$X = 18.873 + 0.02798(D^2L_{\text{avg}})$	0.94
Polystichum munitum	41	$X = -2.5695 + 0.06429(L_{\text{avg}} \times \text{no. fronds})$	0.90
Oxalis oregana	10	$X = 0.4625(\%\text{cover})$	$S_{\bar{X}} = 2.2$

[a] All equations are significant at the 0.99 level. *D*, diameter at litter surface (cm); *L*, length (cm, except for *Acer* = m).
[b] From Russel (1973).

pendent variables, thought to reflect foliage biomass, were selected for each species. Destructive sampling was conducted in the neighborhood of RS-5 and RS-7. Each plant was measured, or cover was estimated, by using a 1-m² sampling frame, and the total foliage was harvested. Excised foliage was placed in ovens within 24 h of harvest, dried for 24 h at 60 °C, and weighed to the nearest gram. Finally, data were plotted and an appropriate function was selected relating foliage weight to the given measurement(s).

Several other species were thinly scattered or present on one or two reference stands. Where similar growth forms and sizes were exhibited over the range of sites investigated, an 'average-tree' sampling procedure was followed (Baskerville 1965). This involved measuring diameter at the litter surface (D) and average stem length (L) and calculating a mean D^2L for all individuals of a given species recorded in the vegetational analysis of a reference stand. Destructive analysis was then performed on selected plants that had characteristics of the mean. The sum of a species foliage biomass in a particular stand was estimated by multiplying the total number recorded by the mean foliage weight. Estimates for ocean spray (*Holodiscus discolor* (Pursh.) Maxim.), hazel (*Corylus cornuta* Marsh. var. *californica* (D.C.) Sharp), and dogwood (*Cornus nuttallii* Aud. ex T. & G.) were made in this manner. Where greater variation in growth form and size occurred, application of the 'average-tree' method was inappropriate. This was the case with red huckleberry (*Vaccinium parvifolium* Smith), which was found scattered through two stands. For this species several plants adjacent to each reference stand covering the range of size classes present in the stand were destructively sampled. From this limited sample, D^2L relationships with leaf weight were roughly established to estimate foliage weights for this species wherever encountered.

To reduce survey time, foliage biomass equations for herb species were not developed. Instead, herbaceous cover was assumed to be directly related to foliage surface area so that 10% cover on a 1-m² plot was equivalent to a one-sided surface area of 0.1 m². This assumption appeared invalid only at very high cover values, not commonly encountered. Only in the case of *Oxalis oregana* Nutt. ex T. & G., which contributed a large amount of surface area to the understory on RS-7 and similar wet sites, was a biomass equation developed (Table 3). Equations relating percentage cover to *total* aboveground biomass for almost all common herbs in the study area exist in Russel (1973).

Converting Biomass to Leaf Area

To estimate leaf area from foliage biomass, a coefficient for each species was required. To accomplish this for needle-leaf species (Table 4), samples were collected from midcrown, with a shotgun where necessary, and surface areas on fresh samples were determined using an optical planimeter (Miller *et al.* 1956; Geppert 1968). Samples were dried for 24 h at 60 °C, then weighed to the nearest 0.1 mg. Finally, all surface areas were corrected for the three-dimensional character of the needles. This was done by projecting a microscope slide of the needle cross section onto paper, then measuring the ratio between the circumference and projected diameter (Drew and Running 1975). From 20 to 25 needles were used for each correction and cross sections were cut from the midpoint of each needle. The red-cedar conversion was adjusted for cross section and leaf-bearing twig weight by multiplying by 1.5. In the case of mountain hemlock (*Tsuga mertensiana*), the *Tsuga heterophylla* coefficient was applied.

Surface areas for broadleaves were obtained by determining similar coefficients (Table 5). Discs of a known diameter were punched from leaves by using various sizes of cork borers. Leaves were picked from a random selection of plants in each reference stand. For the long and narrow leaves of beargrass (*Xerophyllum tenax* (Pursh.) Nutt.) numerous 0.55-cm-diameter discs were punched for about three quarters of the length of each sampled blade. One hundred discs for each species represented on the stand were dried for 24 h at 60 °C and weighed in groups of 10 to the nearest 0.1 mg. All broadleaf surface area figures for major species were corrected for petiolar weight.

Estimating Total Leaf Area from Vegetational Analyses

The vegetation on each reference stand was nondestructively surveyed in late June and July, 1974. This was accomplished for the shrub and herb layers by laying out twenty 4-m² plots, composed of four 1-m² subplots on the inner 30 m × 30 m of the stand. A 10-m-wide buffer strip along each side of the RS was

TABLE 4. Surface area : weight conversions for major tree species

Species	Location[b]	Cross-section factor	Surface Area : Weight (cm²/g)[a] Mean	New	1 year	2 years	3+ years
Pseudotsuga menziesii	N. Oregon Coast[c]	1.18[d]	194.4 (22.7)	202.1 (29.4)	186.7 (13.3)		
	HJA (low elevation)[c]		174.4 (27.9)	204.3 (30.4)	173.2 (21.5)	163.2 (12.5)	148.7 (9.2)
	Ochoco Mtn.[c]		167.1 (22.4)	190.8 (6.5)	179.0 (9.2)	149.1 (17.2)	149.5 (18.3)
	Cache Mtn.[c]		174.7 (26.3)	204.1 (23.2)	177.4 (23.4)	162.8 (17.4)	154.6 (16.6)
Taxus brevifolia	HJA (RS7)	1.07	155.7 (21.2)	186.3 (5.8)	154.7 (11.7)	148.3 (2.7)	133.7 (0.8)
Abies grandis	Cache Mtn.[c]	1.18	131.3 (28.4)	172.3	126.3	119.2	107.4
Tsuga heterophylla	N. Oregon Coast[c]	1.07[d]	173.7 (19.5)	186.7 (13.9)	160.8 (15.7)		
	HJA (low elevation)		203.6 (15.1)	210.0 (12.8)	197.0 (116.2)		
	HJA (RS4)		211.3 (19.6)				
	Wildcat Mtn. Res. Nat. Area[c]		171.5 (20.6)				
Abies procera	HJA (RS4) seedling	1.173 (0.04)	213.3 (12.2)				
	HJA (RS4) overstory	1.158 (0.03)	131.9 (7.0)				
Abies amabilis	HJA (RS4) seedling	1.11 (0.02)	219.4 (6.0)				
	HJA (RS4) overstory	1.16 (0.04)	152.0 (15.1)				
Thuja plicata	HJA (RS7)		176.7 (10.1)				

NOTE: Standard deviations are shown in parentheses.

[a] Conversions are for all sides and include the cross-section corrections.

[b] HJA = H. J. Andrews Experimental Forest, W. Oregon Cascades; Ochoco Mtn. = central Oregon; Cache Mtn. = near east side of the Cascades; Wildcat Mtn. = subalpine true fir stands north of the H. J. Andrews.

[c] Furnished by Gabriel Tucker (unpublished).

[d] Krueger and Ruth (1969) and Drew and Running (1975) arrived at these same figures independently.

TABLE 5. Surface area : weight conversions for common shrubs and herbs in the H. J. Andrews Experimental Forest

Species	RS	Cm^2/g[a]	%Petiole
Acer circinatum	1	603.6 (53.8)	6.28 (1.05)
	5	737.8 (26.4)	
	6	438.4 (50.6)	
	7	688.2 (40.0)	
Berberis nervosa	1	88.4 (4.4)	23.17 (1.91)
	5	176.2 (7.8)	
	6	139.6 (2.8)	
	7	171.2 (5.4)	
Rhododendron macrophyllum	5	261.2 (25.2)	5.40 (1.08)
	6	166.8 (12.6)	
Gaultheria shallon	5	228.0 (14.6)	2.58 (0.76)
	6	166.4 (12.8)	
	7	269.4 (18.8)	
Xerophyllum tenax	4	88.4 (6.0)	0.00
	5	78.0 (4.4)	
	6	77.8 (2.0)	
Polystichum munitum	7	304.6 (6.6)	38.39 (3.90)
Oxalis oregana	7	1193.6 (51.2)	41.77 (2.80)
Castanopsis chrysophylla	6	140.4 (15.0)	2.73 (0.87)
Corylus cornuta calif.	1	424.2 (28.8)	N.A.[b]
Holodiscus discolor	1	420.6 (28.4)	N.A.
Cornus canadensis	4	245.8 (20.8)	N.A.
Vaccinium parvifolium	7	514.0 (15.2)	N.A.
Achyls triphylla	4	856.4 (38.4)	N.A.
	7	798.0 (78.2)	
Linnaea borealis	7	561.2 (9.4)	N.A.
Chimaphila umbellata	2	252.4 (9.8)	N.A.
	7	213.0 (8.8)	
Cornus nuttallii	6	350.6 (33.4)	3.12 (0.35)
Coptis laciniata	2	599.0 (19.6)	N.A.

NOTE: Standard deviations are shown in parentheses.
[a] All values are for two sides
[b] N.A., not available

not surveyed because of frequent disturbances there. Appropriate variables were measured for each species encountered. Cover for *Oxalis*, Oregon grape (*Berberis nervosa* Pursh.), salal (*Gaultheria shallon* Pursh.), and the herb layer was estimated on each subplot and an average was computed for the entire plot. Foliage biomass for tree species was computed for the full 50 m × 50 m area from diameter data collected by International Biological Program (IBP) personnel.[3] These data were used with the regressions of leaf dry weight on diameter at breast height (DBH) to compute species foliage biomass. Coefficients were applied to foliage dry weights to determine leaf area by species in square metres per square metre. Values for individual species were summed to obtain totals for each reference stand.

Results

The total foliage biomass, surface area, and percentage surface area in the shrub and herb layers for each of the six stands are presented in Fig. 2. The location of the values in Fig. 2 corresponds to the environmental location of each reference stand as presented in Fig. 1.

The coniferous needle surface area coeffi-

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[3] Unpublished data on file at the Coniferous Forest Biome Data Bank, Oregon State University, Forest Research Laboratory.

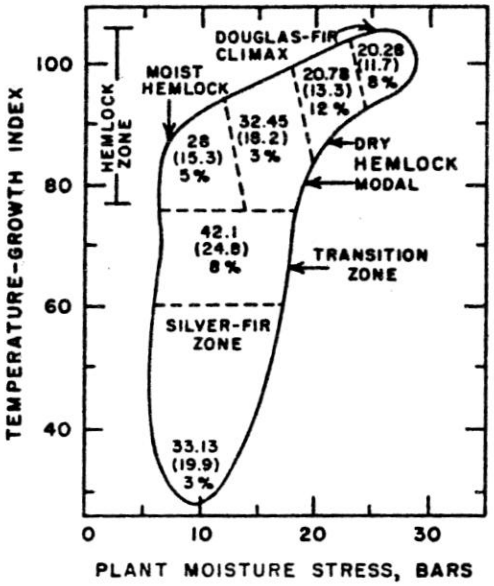

FIG. 2. Total foliage biomass (mt/ha, parenthetical values), total leaf area (m^2/m^2, upper values), and percentage of the total surface area in the shrubs and herbs (lower values) for the six reference stands superimposed on Fig. 1. Projected leaf areas, one side with no cross-section corrections, are as follows: RS-1, 8.7 m^2/m^2; RS-2, 14.3; RS-4, 14.4; RS-5, 18.6; RS-6, 9.1; RS-7, 12.0. Sugar pine (*Pinus lambertiana* Dougl.) would add about 0.4 mt/ha to RS-1 and 0.9 mt/ha to RS-6, but it is not included here because there is no surface area conversion available.

cients (Table 4) show that surface area per gram of needle decreased substantially with increasing age, although not all age class values are statistically different. In old-growth Douglas fir, where about 20% of the total foliage was current, 15% 1 year old, 15% 2 years old, and 50% 3 years or older, the surface area decreased from about 204 cm^2/g for the current foliage to 149 cm^2/g for the 3rd year and older foliage (statistically different at the 0.95 level). This suggests that substantial errors may result from not treating age classes separately. However, because of inadequate data, only a few species other than Douglas fir had leaf areas computed by age class.

Also, silver and noble fir growing in the understory had a greater surface area per gram than those in the overstory (Table 4). We expect that this is also true for western hemlock and other species, which suggests in addition that a variety of coefficients may be obtained from various areas of the crowns of the large overstory trees.

Broad-leaved species illustrate a greater range of coefficients than the conifers (Table 5). For example, beargrass had 77 cm^2/g, whereas *Oxalis* had 1194 cm^2/g. Likewise, there is a wide range of values within a single species. For example, vine maple (*Acer circinatum* Pursh.) ranged from 438 cm^2/g to 738 cm^2/g, and salal from 166 cm^2/g to 269 cm^2/g.

Discussion

In observing forests with different leaf areas one may question whether these differences are associated with environmental adaptations or are merely changes associated with stand development. There is general support for rapid increase in leaf area from the time of establishment until crown closure. This period may be as short as 4 years in eastern deciduous forests (Marks 1974) or may extend beyond a decade as reported in a white pine (*Pinus strobus* L.) plantation by Swank and Schreuder (1973). After closure the amounts of foliage may return to a somewhat lower plateau (Kira and Shidei 1967; Ovington 1957).

The reported peaks are, however, not always convincing and may be offset by unreported increases in understory foliage development of older forests. We can probably assume, barring major windstorms, fire, or other recent acute disturbances, that old-growth forest communities do exhibit equilibrium leaf areas. Whether this is greater or less than that at the time of crown closure awaits confirmation.

In this study the magnitude of the leaf areas estimated for midelevation stands was higher than those associated with cooler or warmer environments with similar moisture regimes (Fig. 2). In fact, the value 42.1 m^2/m^2 (projected leaf area of 18.6) for reference stand 5 is near the maximum ever reported. Westman and Whittaker (1975) recently reported a similar value for a mature coast redwood forest in California. In a 26-year-old hemlock forest on the Oregon Coast, Fujimori (1971) estimated foliage at 21.1 mt/ha which converts to 37 m^2/m^2 of total leaf area using the appropriate coefficient from Table 4.

What permits such a large accumulation of foliage to develop in an area of summer drought?

In the humid deciduous forests of the eastern United States, total leaf areas above 12 m^2/m^2 are uncommon (Whittaker 1966). Even in a tropical rain forest of Thailand an exceptional total leaf area of 32 m^2/m^2 was reported, with most plots supporting less than 24 m^2/m^2 (Ogawa *et al.* 1965).

From the moisture gradient defined directly by the stress experienced by understory conifers (Fig. 2), it is clear that soil water is not very limiting to the forest communities where the highest foliage areas accumulate.

Apparently, temperature is the variable which permits large accumulations of foliage, but neither the warmest sites nor those with the longest growing season support the largest amount of foliage. Rather, we hypothesize that it is a special balance of temperatures that favors modest respiration rates but yet permits, even during the dormant season, considerable net photosynthesis. In the redwood forests of California, the Coast Range forests of the Pacific Northwest, and the midelevation forests of the western Cascades, the winter temperatures are usually above freezing, at least during the day (Waring and Major 1964; Zobel *et al.* 1973). Where there is a snowpack, day temperatures usually remain above −2 °C so the water column in the stem is not often frozen (Zimmerman 1964) and both transpiration and photosynthesis can occur. During the summer, coastal fog, maritime air, or elevational-related cooling create mild growing-season temperatures around 10 °C (Waring and Major 1964; Zobel *et al.* 1973). For conifers these temperatures permit very respectable rates of photosynthesis (Walker *et al.* 1972).

This proposed explanation could also account for the decrease in leaf area in well watered but warmer habitats where respiration increases substantially (RS-2 and RS-7). At higher elevations colder winter temperatures and a shorter growing season notably limit photosynthesis (Emmingham 1974) and together with snow damage could explain the lower value found there.

There are some special problems associated with estimating leaf area which also merit discussion. First of all is an inconsistency in expressing results. Usually data from broadleaf species have been reported as representing only a single surface. This is not a major problem if the convention is clearly noted by the authors. We have freely converted many of the values reported by Whittaker (1966), Westman and Whittaker (1975), and Ogawa *et al.* (1965) to total surface area. There is real difficulty, however, when data for needle-leaf species are reported inconsistently on both a projected and total surface area basis. The problem becomes acute when both broadleaf and needle-leaf species occurring in the same stand are reported differently. We believe there is need to standardize, and because stomata and energy exchange can occur on more than one leaf surface, we feel total surface area is the most desirable expression. From recent studies comes further support that interception, photosynthesis, respiration, and possibly even foliar nutrient concentrations are biologically best interpreted in such context (Linder 1974; Sollins *et al.* 1974; Gholz, unpublished).

A second problem in estimating surface area is converting from biomass data. For example, in Table 5, differences in species coefficients range from 77 cm^2/g to 1194 cm^2/g, with further variation noted within a species, e.g., *Acer circinatum*. Recent unpublished studies by Gholz suggest much of the within-species variation is a response to development under different light regimes. Light has similarly been attributed as the causal factor in explaining leaf area–weight differences in European beech (Kira *et al.* 1969) and a variety of oak–hickory forest species (Monk *et al.* 1970). These follow earlier classical experimental work (e.g., Blackman and Rutter 1948).

Additionally, there are differences in leaf area–weight coefficients as leaves age. This point was made earlier in discussing Table 4. For both problems, development of separate regression equations for individual stands is a possible but, as we found, laborious solution.

Where possible, we recommend a direct estimation of leaf area, bypassing the difficulties of converting from foliar biomass. This appears possible from simple linear relationships, such as recently discovered between cross-sectional area of functional conducting tissue in the stem and leaf weight or area (Grier and Waring 1974; Dixon 1971). More recently, Waring *et al.* (unpublished) found a similar linear coefficient for shrub species *Rhododendron macrophyllum*.

These new coefficients may solve another problem common to estimating foliar area of trees. Ogawa *et al.* (1965), Kira and Shidei (1967), and Shinozaki *et al.* (1964) reported that estimates of foliage weight from measurements of stem diameter were often overestimates, especially for larger trees. Some of this may be a result of competition among trees (Satoo 1966). This could also occur by extrapolating from small trees which contain only conducting tissue to large trees with nonconducting heartwood. In this study, regression equations were developed from data including large trees. Still, because of the log relationships, a small change in stem diameter suggests a fairly large change in leaf weight and area. Direct measurement of linear coefficients could result in a considerable gain in accuracy.

Increasingly, accurate estimates of leaf area are necessary to test ecological hypotheses concerning the functional recovery of ecosystems. How long recovery takes is often a function of reestablishment of leaf area, sometimes by shrub rather than tree species. As the importance of understory species in nutrient cycling has become better appreciated, accurate estimates of their contribution to uptake, storage, and litter fall are needed. With the development of accurate methods, we hope quantitative estimates of leaf area will become more commonly reported in vegetational analyses.

In summary, when the total leaf areas of six old-growth forest communities in western Oregon were estimated, differences were observed which were attributed mainly to variations in the physical environment. The highest values may represent maximum accumulation and reflect particular combinations of environment that permit adequate photosynthesis with modest respiration in maritime-influenced cool temperate forests of the Pacific Northwest. Methods developed in this paper will enable ecologists to explore further the foliage relations of both disturbed and undisturbed plant communities.

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Leaf area differences associated with old-growth forest communities in the western Oregon Cascades[1]

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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. Can. J. For. Res. **6**: 49–57.

Total leaf area varied from 20 to 42 m^2/m^2 in 250- to 450-year-old forest communities developed under different temperature and moisture conditions. The largest values were in communities at midelevations where winter snowpack accumulated and growing-season temperatures were cool. Shrub and herb leaf area varied from 3% to 14% of the total. Equations for converting from foliage biomass to surface area are included for most species encountered.

GHOLZ, H. L., F. K. FITZ et 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.

La surface foliaire totale variait de 20–42 m^2/m^2 dans des groupements forestiers âgés de 250–450 ans formés sous diverses conditions de température et d'humidité. Les valeurs les plus fortes ont été observées dans les peuplements situés à mi-élévation, où la neige s'accumule en hiver et où les températures de la saison de croissance sont fraîches. La surface foliaire des arbustes et des herbes variait de 3% à 4% de la surface foliaire totale. L'article fournit des équations de conversion de la biomasse de feuillage à la surface foliaire pour la plupart des espèces qui s'y rencontrent.

[Traduit par le journal]

Introduction

Leaf area and its spatial distribution is essential for estimating photosynthesis, transpiration, respiration, canopy interception, and energy transmission to the ground. Thus, it is a basic structural feature required in all terrestrial ecosystem studies.

This study had two major objectives: (1) to develop techniques enabling one to assess foliage areas for a wide variety of species characteristic of forest communities in the Cascade Mountains of western Oregon, and (2) to evaluate whether leaf area differences among major vegetational units are associated with measured moisture and temperature gradients.

Study Areas

The study was confined to the H. J. Andrews Experimental Forest, a 6000-ha watershed 60 km east of Eugene, Oregon (44° N, 122° W). Dyrness *et al.* (1974) recognized 23 mature forest communities there, and Zobel *et al.* (1974) described their ecological distributions in terms of measured gradients of plant moisture stress (Waring and Cleary 1967) and temperature (Cleary and Waring 1969) (Fig. 1). 'Reference stands' (RS) representing the major communities were established for detailed analysis (Zobel *et al.* 1974). To assess possible differences in leaf area, six reference stands representing a broad spectrum of environments were selected. Descriptions of these stands are given in Table 1 and their locations in environmental coordinates are designated in Fig. 1. In all stands 250- to 450-year-old Douglas fir (*Pseudotsuga menziesii* (Mirb) Franco var. *menziesii*) was the major overstory tree, constituting from 55 to 98% of the total tree foliage biomass.

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TABLE 1. Descriptions of six stands (RS) studied

RS	Community	Elevation, m	Description
1	*Pseudotsuga menziesii / Holodiscus discolor* (PSME/HODI)	490	Hot, dry; Douglas-fir climax
2	*Tsuga heterophylla / Rhododendron macrophyllum / Berberis nervosa* (TSHE/RHMA/BENE)	490	Modal; hemlock climax
4	*Abies amabilis / Tiarella unifolia* (ABAM/TIUN)	1310	Subalpine; silver-fir climax
5	*Tsuga heterophylla – Abies amabilis / Rhododendron macrophyllum / Berberis nervosa* (TSHE–ABAM/RHMA/BENE)	885	Midelevation; hemlock / silver-fir climax
6	*Tsuga heterophylla / Castanopsis chrysophylla* (TSHE/CACH)	610	Dry; hemlock climax
7	*Tsuga heterophylla / Polystichum munitum / Oxalis oregana* (TSHE/POMU/OXOR)	490	Very wet; hemlock climax

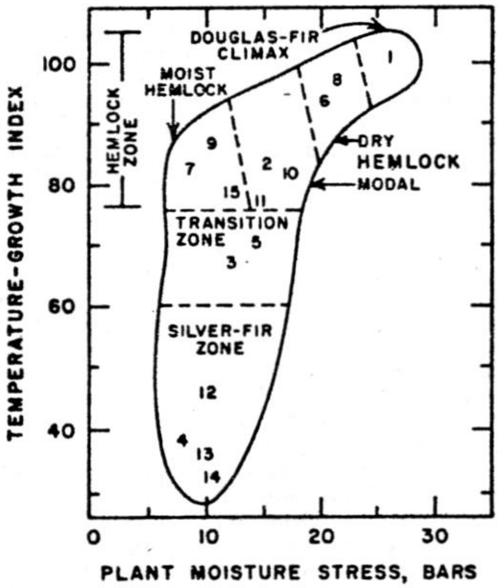

FIG. 1. Distribution of plant communities in the H. J. Andrews Experimental Forest (after Zobel *et al.* 1974). Moisture stress gradient represents predawn measurements when soil water reserves were minimal for the year. The temperature gradient is a physiological assessment of daily air and soil temperatures throughout the growing season for Douglas fir. Numbers refer to reference stands where detailed analysis of vegetation and environment were made.

TABLE 2. Regression equation constants for foliage biomass of major tree species[a]

Species	A	B	R^2
P. menziesii	−3.890	1.890	**0.88**
T. heterophylla	−4.195	2.119	**0.96**
A. amabilis	−5.480	2.380	**0.97**
A. procera	−4.990	2.190	**0.99**
T. plicata	2.0997	1.915	**0.99**
C. chrysophylla	−3.0258	1.607	**0.79**

[a] All equations are of the form ln(dry foliage wt.) = **A + B** ln(DBH). Dry foliage wt. is in kilograms, DBH is in centimetres.

Methods

Estimating Foliar Biomass (see Tables 2 and 3)

Because most foliage data from coniferous forests are reported as biomass, one must first use mensurational techniques to estimate biomass and then convert to leaf area.

Grier (unpublished) furnished foliage biomass equations for Douglas fir, golden chinkapin (*Castanopsis chrysophylla* (Dougl.) A. DC.), and noble fir (*Abies procera* Rehd.). The equation for western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) was derived from a composite of data from Krumlik (1974) and Fujimori (1971). The equation for silver fir (*Abies amabilis* (Dougl. Forbes) was derived from a composite of data from Krumlik (1974) and Grier (unpublished). Foliage biomass for western red cedar (*Thuja plicata* Donn.) was calculated using a common logarithm equation for *Thuja occidentalis* L. (Reiners 1972). Foliage biomass for mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), a minor overstory conifer, and Pacific yew (*Taxus brevifolia* Nutt.), a minor understory conifer, was estimated using the equation for western hemlock. For sugar pine (*Pinus lambertiana* Dougl.), foliage biomass was estimated from the Douglas fir equation.

For the seven most abundant shrubs, methods were sought that would allow rapid, objective, and accurate estimates of foliage biomass. Easily measurable inde-

TABLE 3. Understory foliage biomass equations

Species	Sample size	Equation[a]	R^2
Acer circinatum[b]	132	$X = 9.03(D^2L_{\max})^{\frac{1}{2}}$	0.90
Berberis nervosa	32	$X = 14.218+1.984(\%\text{cover})$	0.80
Rhododendron macrophyllum	40	$\ln(X) = 0.067177 + 0.60981 \ln(D^2L_{\max})$	0.90
Gaultheria shallon	32	$\ln(X) = 1.5137 + 0.70263 \ln(\%\text{cover})$	0.83
Xerophyllum tenax	22	$X = 18.873 + 0.02798(D^2L_{\text{avg}})$	0.94
Polystichum munitum	41	$X = -2.5695 + 0.06429(L_{\text{avg}} \times \text{no. fronds})$	0.90
Oxalis oregana	10	$X = 0.4625(\%\text{cover})$	$S_{\bar{X}} = 2.2$

[a] All equations are significant at the 0.99 level. *D*, diameter at litter surface (cm); *L*, length (cm, except for *Acer* = m).
[b] From Russel (1973).

pendent variables, thought to reflect foliage biomass, were selected for each species. Destructive sampling was conducted in the neighborhood of RS-5 and RS-7. Each plant was measured, or cover was estimated, by using a 1-m² sampling frame, and the total foliage was harvested. Excised foliage was placed in ovens within 24 h of harvest, dried for 24 h at 60 °C, and weighed to the nearest gram. Finally, data were plotted and an appropriate function was selected relating foliage weight to the given measurement(s).

Several other species were thinly scattered or present on one or two reference stands. Where similar growth forms and sizes were exhibited over the range of sites investigated, an 'average-tree' sampling procedure was followed (Baskerville 1965). This involved measuring diameter at the litter surface (D) and average stem length (L) and calculating a mean D^2L for all individuals of a given species recorded in the vegetational analysis of a reference stand. Destructive analysis was then performed on selected plants that had characteristics of the mean. The sum of a species foliage biomass in a particular stand was estimated by multiplying the total number recorded by the mean foliage weight. Estimates for ocean spray (*Holodiscus discolor* (Pursh.) Maxim.), hazel (*Corylus cornuta* Marsh. var. *californica* (D.C.) Sharp), and dogwood (*Cornus nuttallii* Aud. ex T. & G.) were made in this manner. Where greater variation in growth form and size occurred, application of the 'average-tree' method was inappropriate. This was the case with red huckleberry (*Vaccinium parvifolium* Smith), which was found scattered through two stands. For this species several plants adjacent to each reference stand covering the range of size classes present in the stand were destructively sampled. From this limited sample, D^2L relationships with leaf weight were roughly established to estimate foliage weights for this species wherever encountered.

To reduce survey time, foliage biomass equations for herb species were not developed. Instead, herbaceous cover was assumed to be directly related to foliage surface area so that 10% cover on a 1-m² plot was equivalent to a one-sided surface area of 0.1 m². This assumption appeared invalid only at very high cover values, not commonly encountered. Only in the case of *Oxalis oregana* Nutt. ex T. & G., which contributed a large amount of surface area to the understory on RS-7 and similar wet sites, was a biomass equation developed (Table 3). Equations relating percentage cover to *total* aboveground biomass for almost all common herbs in the study area exist in Russel (1973).

Converting Biomass to Leaf Area

To estimate leaf area from foliage biomass, a coefficient for each species was required. To accomplish this for needle-leaf species (Table 4), samples were collected from midcrown, with a shotgun where necessary, and surface areas on fresh samples were determined using an optical planimeter (Miller *et al.* 1956; Geppert 1968). Samples were dried for 24 h at 60 °C, then weighed to the nearest 0.1 mg. Finally, all surface areas were corrected for the three-dimensional character of the needles. This was done by projecting a microscope slide of the needle cross section onto paper, then measuring the ratio between the circumference and projected diameter (Drew and Running 1975). From 20 to 25 needles were used for each correction and cross sections were cut from the midpoint of each needle. The red-cedar conversion was adjusted for cross section and leaf-bearing twig weight by multiplying by 1.5. In the case of mountain hemlock (*Tsuga mertensiana*), the *Tsuga heterophylla* coefficient was applied.

Surface areas for broadleaves were obtained by determining similar coefficients (Table 5). Discs of a known diameter were punched from leaves by using various sizes of cork borers. Leaves were picked from a random selection of plants in each reference stand. For the long and narrow leaves of beargrass (*Xerophyllum tenax* (Pursh.) Nutt.) numerous 0.55-cm-diameter discs were punched for about three quarters of the length of each sampled blade. One hundred discs for each species represented on the stand were dried for 24 h at 60 °C and weighed in groups of 10 to the nearest 0.1 mg. All broadleaf surface area figures for major species were corrected for petiolar weight.

Estimating Total Leaf Area from Vegetational Analyses

The vegetation on each reference stand was nondestructively surveyed in late June and July, 1974. This was accomplished for the shrub and herb layers by laying out twenty 4-m² plots, composed of four 1-m² subplots on the inner 30 m × 30 m of the stand. A 10-m-wide buffer strip along each side of the RS was

TABLE 4. Surface area : weight conversions for major tree species

Species	Location[b]	Cross-section factor	Surface Area : Weight (cm²/g)[a]				
			Mean	New	1 year	2 years	3+ years
Pseudotsuga menziesii	N. Oregon Coast[c]	1.18[d]	194.4 (22.7)	202.1 (29.4)	186.7 (13.3)		
	HJA (low elevation)[c]		174.4 (27.9)	204.3 (30.4)	173.2 (21.5)	163.2 (12.5)	148.7 (9.2)
	Ochoco Mtn.[c]		167.1 (22.4)	190.8 (6.5)	179.0 (9.2)	149.1 (17.2)	149.5 (18.3)
	Cache Mtn.[c]		174.7 (26.3)	204.1 (23.2)	177.4 (23.4)	162.8 (17.4)	154.6 (16.6)
Taxus brevifolia	HJA (RS7)	1.07	155.7 (21.2)	186.3 (5.8)	154.7 (11.7)	148.3 (2.7)	133.7 (0.8)
Abies grandis	Cache Mtn.[c]	1.18	131.3 (28.4)	172.3	126.3	119.2	107.4
Tsuga heterophylla	N. Oregon Coast[c]	1.07[d]	173.7 (19.5)	186.7 (13.9)	160.8 (15.7)		
	HJA (low elevation)		203.6 (15.1)	210.0 (12.8)	197.0 (116.2)		
	HJA (RS4)		211.3 (19.6)				
	Wildcat Mtn. Res. Nat. Area[c]		171.5 (20.6)				
Abies procera	HJA (RS4) seedling	1.173 (0.04)	213.3 (12.2)				
	HJA (RS4) overstory	1.158 (0.03)	131.9 (7.0)				
Abies amabilis	HJA (RS4) seedling	1.11 (0.02)	219.4 (6.0)				
	HJA (RS4) overstory	1.16 (0.04)	152.0 (15.1)				
Thuja plicata	HJA (RS7)		176.7 (10.1)				

NOTE: Standard deviations are shown in parentheses.

[a] Conversions are for all sides and include the cross-section corrections.

[b] HJA = H. J. Andrews Experimental Forest, W. Oregon Cascades; Ochoco Mtn. = central Oregon; Cache Mtn. = near east side of the Cascades; Wildcat Mtn. = subalpine true fir stands north of the H. J. Andrews.

[c] Furnished by Gabriel Tucker (unpublished).

[d] Krueger and Ruth (1969) and Drew and Running (1975) arrived at these same figures independently.

TABLE 5. Surface area : weight conversions for common shrubs and herbs in the H. J. Andrews Experimental Forest

Species	RS	Cm^2/g^a	%Petiole
Acer circinatum	1	603.6 (53.8)	
	5	737.8 (26.4)	
	6	438.4 (50.6)	6.28 (1.05)
	7	688.2 (40.0)	
Berberis nervosa	1	88.4 (4.4)	
	5	176.2 (7.8)	
	6	139.6 (2.8)	23.17 (1.91)
	7	171.2 (5.4)	
Rhododendron macrophyllum	5	261.2 (25.2)	
	6	166.8 (12.6)	5.40 (1.08)
Gaultheria shallon	5	228.0 (14.6)	
	6	166.4 (12.8)	2.58 (0.76)
	7	269.4 (18.8)	
Xerophyllum tenax	4	88.4 (6.0)	
	5	78.0 (4.4)	0.00
	6	77.8 (2.0)	
Polystichum munitum	7	304.6 (6.6)	38.39 (3.90)
Oxalis oregana	7	1193.6 (51.2)	41.77 (2.80)
Castanopsis chrysophylla	6	140.4 (15.0)	2.73 (0.87)
Corylus cornuta calif.	1	424.2 (28.8)	N.A.[b]
Holodiscus discolor	1	420.6 (28.4)	N.A.
Cornus canadensis	4	245.8 (20.8)	N.A.
Vaccinium parvifolium	7	514.0 (15.2)	N.A.
Achyls triphylla	4	856.4 (38.4)	
	7	798.0 (78.2)	N.A.
Linnaea borealis	7	561.2 (9.4)	N.A.
Chimaphila umbellata	2	252.4 (9.8)	
	7	213.0 (8.8)	N.A.
Cornus nuttallii	6	350.6 (33.4)	3.12 (0.35)
Coptis laciniata	2	599.0 (19.6)	N.A.

NOTE: Standard deviations are shown in parentheses.
[a] All values are for two sides
[b] N.A., not available

not surveyed because of frequent disturbances there. Appropriate variables were measured for each species encountered. Cover for *Oxalis*, Oregon grape (*Berberis nervosa* Pursh.), salal (*Gaultheria shallon* Pursh.), and the herb layer was estimated on each subplot and an average was computed for the entire plot. Foliage biomass for tree species was computed for the full 50 m × 50 m area from diameter data collected by International Biological Program (IBP) personnel.[3] These data were used with the regressions of leaf dry weight on diameter at breast height (DBH) to compute species foliage biomass. Coefficients were applied to foliage dry weights to determine leaf area by species in square metres per square metre. Values for individual species were summed to obtain totals for each reference stand.

Results

The total foliage biomass, surface area, and percentage surface area in the shrub and herb layers for each of the six stands are presented in Fig. 2. The location of the values in Fig. 2 corresponds to the environmental location of each reference stand as presented in Fig. 1.

The coniferous needle surface area coeffi-

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[3] Unpublished data on file at the Coniferous Forest Biome Data Bank, Oregon State University, Forest Research Laboratory.

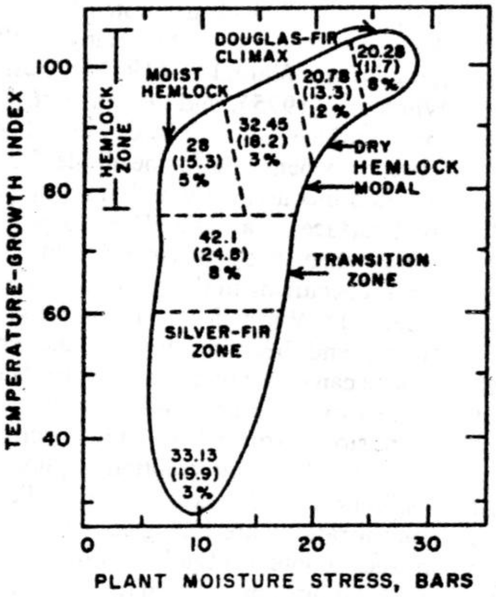

FIG. 2. Total foliage biomass (mt/ha, parenthetical values), total leaf area (m^2/m^2, upper values), and percentage of the total surface area in the shrubs and herbs (lower values) for the six reference stands superimposed on Fig. 1. Projected leaf areas, one side with no cross-section corrections, are as follows: RS-1, 8.7 m^2/m^2; RS-2, 14.3; RS-4, 14.4; RS-5, 18.6; RS-6, 9.1; RS-7, 12.0. Sugar pine (*Pinus lambertiana* Dougl.) would add about 0.4 mt/ha to RS-1 and 0.9 mt/ha to RS-6, but it is not included here because there is no surface area conversion available.

cients (Table 4) show that surface area per gram of needle decreased substantially with increasing age, although not all age class values are statistically different. In old-growth Douglas fir, where about 20% of the total foliage was current, 15% 1 year old, 15% 2 years old, and 50% 3 years or older, the surface area decreased from about 204 cm^2/g for the current foliage to 149 cm^2/g for the 3rd year and older foliage (statistically different at the 0.95 level). This suggests that substantial errors may result from not treating age classes separately. However, because of inadequate data, only a few species other than Douglas fir had leaf areas computed by age class.

Also, silver and noble fir growing in the understory had a greater surface area per gram than those in the overstory (Table 4). We expect that this is also true for western hemlock and other species, which suggests in addition that a variety of coefficients may be obtained from various areas of the crowns of the large overstory trees.

Broad-leaved species illustrate a greater range of coefficients than the conifers (Table 5). For example, beargrass had 77 cm^2/g, whereas *Oxalis* had 1194 cm^2/g. Likewise, there is a wide range of values within a single species. For example, vine maple (*Acer circinatum* Pursh.) ranged from 438 cm^2/g to 738 cm^2/g, and salal from 166 cm^2/g to 269 cm^2/g.

Discussion

In observing forests with different leaf areas one may question whether these differences are associated with environmental adaptations or are merely changes associated with stand development. There is general support for rapid increase in leaf area from the time of establishment until crown closure. This period may be as short as 4 years in eastern deciduous forests (Marks 1974) or may extend beyond a decade as reported in a white pine (*Pinus strobus* L.) plantation by Swank and Schreuder (1973). After closure the amounts of foliage may return to a somewhat lower plateau (Kira and Shidei 1967; Ovington 1957).

The reported peaks are, however, not always convincing and may be offset by unreported increases in understory foliage development of older forests. We can probably assume, barring major windstorms, fire, or other recent acute disturbances, that old-growth forest communities do exhibit equilibrium leaf areas. Whether this is greater or less than that at the time of crown closure awaits confirmation.

In this study the magnitude of the leaf areas estimated for midelevation stands was higher than those associated with cooler or warmer environments with similar moisture regimes (Fig. 2). In fact, the value 42.1 m^2/m^2 (projected leaf area of 18.6) for reference stand 5 is near the maximum ever reported. Westman and Whittaker (1975) recently reported a similar value for a mature coast redwood forest in California. In a 26-year-old hemlock forest on the Oregon Coast, Fujimori (1971) estimated foliage at 21.1 mt/ha which converts to 37 m^2/m^2 of total leaf area using the appropriate coefficient from Table 4.

What permits such a large accumulation of foliage to develop in an area of summer drought?

In the humid deciduous forests of the eastern United States, total leaf areas above 12 m^2/m^2 are uncommon (Whittaker 1966). Even in a tropical rain forest of Thailand an exceptional total leaf area of 32 m^2/m^2 was reported, with most plots supporting less than 24 m^2/m^2 (Ogawa *et al.* 1965).

From the moisture gradient defined directly by the stress experienced by understory conifers (Fig. 2), it is clear that soil water is not very limiting to the forest communities where the highest foliage areas accumulate.

Apparently, temperature is the variable which permits large accumulations of foliage, but neither the warmest sites nor those with the longest growing season support the largest amount of foliage. Rather, we hypothesize that it is a special balance of temperatures that favors modest respiration rates but yet permits, even during the dormant season, considerable net photosynthesis. In the redwood forests of California, the Coast Range forests of the Pacific Northwest, and the midelevation forests of the western Cascades, the winter temperatures are usually above freezing, at least during the day (Waring and Major 1964; Zobel *et al.* 1973). Where there is a snowpack, day temperatures usually remain above —2 °C so the water column in the stem is not often frozen (Zimmerman 1964) and both transpiration and photosynthesis can occur. During the summer, coastal fog, maritime air, or elevational-related cooling create mild growing-season temperatures around 10 °C (Waring and Major 1964; Zobel *et al.* 1973). For conifers these temperatures permit very respectable rates of photosynthesis (Walker *et al.* 1972).

This proposed explanation could also account for the decrease in leaf area in well watered but warmer habitats where respiration increases substantially (RS-2 and RS-7). At higher elevations colder winter temperatures and a shorter growing season notably limit photosynthesis (Emmingham 1974) and together with snow damage could explain the lower value found there.

There are some special problems associated with estimating leaf area which also merit discussion. First of all is an inconsistency in expressing results. Usually data from broadleaf species have been reported as representing only a single surface. This is not a major problem if the convention is clearly noted by the authors. We have freely converted many of the values reported by Whittaker (1966), Westman and Whittaker (1975), and Ogawa *et al.* (1965) to total surface area. There is real difficulty, however, when data for needle-leaf species are reported inconsistently on both a projected and total surface area basis. The problem becomes acute when both broadleaf and needle-leaf species occurring in the same stand are reported differently. We believe there is need to standardize, and because stomata and energy exchange can occur on more than one leaf surface, we feel total surface area is the most desirable expression. From recent studies comes further support that interception, photosynthesis, respiration, and possibly even foliar nutrient concentrations are biologically best interpreted in such context (Linder 1974; Sollins *et al.* 1974; Gholz, unpublished).

A second problem in estimating surface area is converting from biomass data. For example, in Table 5, differences in species coefficients range from 77 cm^2/g to 1194 cm^2/g, with further variation noted within a species, e.g., *Acer circinatum*. Recent unpublished studies by Gholz suggest much of the within-species variation is a response to development under different light regimes. Light has similarly been attributed as the causal factor in explaining leaf area–weight differences in European beech (Kira *et al.* 1969) and a variety of oak–hickory forest species (Monk *et al.* 1970). These follow earlier classical experimental work (e.g., Blackman and Rutter 1948).

Additionally, there are differences in leaf area–weight coefficients as leaves age. This point was made earlier in discussing Table 4. For both problems, development of separate regression equations for individual stands is a possible but, as we found, laborious solution.

Where possible, we recommend a direct estimation of leaf area, bypassing the difficulties of converting from foliar biomass. This appears possible from simple linear relationships, such as recently discovered between cross-sectional area of functional conducting tissue in the stem and leaf weight or area (Grier and Waring 1974; Dixon 1971). More recently, Waring *et al.* (unpublished) found a similar linear coefficient for shrub species *Rhododendron macrophyllum*.

These new coefficients may solve another problem common to estimating foliar area of trees. Ogawa *et al.* (1965), Kira and Shidei (1967), and Shinozaki *et al.* (1964) reported that estimates of foliage weight from measurements of stem diameter were often overestimates, especially for larger trees. Some of this may be a result of competition among trees (Satoo 1966). This could also occur by extrapolating from small trees which contain only conducting tissue to large trees with nonconducting heartwood. In this study, regression equations were developed from data including large trees. Still, because of the log relationships, a small change in stem diameter suggests a fairly large change in leaf weight and area. Direct measurement of linear coefficients could result in a considerable gain in accuracy.

Increasingly, accurate estimates of leaf area are necessary to test ecological hypotheses concerning the functional recovery of ecosystems. How long recovery takes is often a function of reestablishment of leaf area, sometimes by shrub rather than tree species. As the importance of understory species in nutrient cycling has become better appreciated, accurate estimates of their contribution to uptake, storage, and litter fall are needed. With the development of accurate methods, we hope quantitative estimates of leaf area will become more commonly reported in vegetational analyses.

In summary, when the total leaf areas of six old-growth forest communities in western Oregon were estimated, differences were observed which were attributed mainly to variations in the physical environment. The highest values may represent maximum accumulation and reflect particular combinations of environment that permit adequate photosynthesis with modest respiration in maritime-influenced cool temperate forests of the Pacific Northwest. Methods developed in this paper will enable ecologists to explore further the foliage relations of both disturbed and undisturbed plant communities.

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