

A 400-year-old Douglas fir tree and its epiphytes: biomass, surface area, and their distributions

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Methods have been developed to yield total tree estimates of biomass for various components of a tree (trunk, axes, twigs, and needles) and its community of epiphytes (microorganisms, lichens, and bryophytes). Trees were sampled with the help of climbing techniques modified from mountain climbing. Two stages of sampling were involved. First, all units of the population were described so that their weights could be predicted. Second, several units were chosen with probability of selection dependent upon predicted weight and sampled in detail. Biomass estimates from the sampled units were expanded to tree totals with information gathered during the first sampling stage. Internal structure of the crown (tree components and epiphytes) is illustrated by maps of trunk and branch systems and by diagrams of horizontal and vertical distributions. This internal structure was also derived from the first sampling stage.

These methods have been applied to nine old-growth Douglas fir trees (*Pseudotsuga menziesii* (Mirb.) Franco). Data from a single 400-year-old tree (1.46 m dbh, 77 m in height) in the H. J. Andrews Experimental Forest in the western Cascade Mountains of Oregon are presented. Biomass and surface area estimates are as follows: trunk, 26 870 kg, 223 m²; axes (>4 cm), 1530 kg, 81 m²; living twigs (<4 cm), 480 kg, 373 m²; dead twigs, 78 kg, 104 m²; needles, 198 kg, 2860 m²; lichens, 13.1 kg; and bryophytes, 4.7 kg. Total cell volume of microepiphytes on twigs was estimated to have been 300 cm³ and total cover by microepiphytes on needles was estimated to have been 191 m².

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Des méthodes ont été développées permettant l'estimation totale de la biomasse des divers composants de l'arbre (tronc, axes, brindilles et aiguilles) et de ses communautés d'épiphytes (micro-organismes, lichens et bryophytes). Les arbres ont été échantillonnés à l'aide de techniques d'escalade analogues à celles utilisées en montagne. L'échantillonnage a été fait en deux stades: au cours du premier stade toutes les unités de population ont été décrites de telle sorte que leurs poids ont pu être prédits. Au cours du deuxième stade, quelques unités destinées à être étudiées en détail ont été choisies en utilisant une probabilité dérivée du poids prédit. L'estimation de la biomasse des unités échantillonnées a ensuite été étendue à l'estimation de tous les composants de l'arbre en se servant de l'information obtenue au cours du premier stade de l'échantillonnage. La structure interne de l'arbre (composants et épiphytes) est illustrée par des cartes du tronc et de ses branches et par des diagrammes de distribution verticale et horizontale. Cette structure interne dérive également du premier stade d'échantillonnage.

Ces méthodes ont été utilisées pour neuf sapins Douglas (*Pseudotsuga menziesii* (Mirb.) Franco). Les données obtenues pour l'un d'entre eux, un arbre âgé de 400 ans (1.46 m diamètre à hauteur de poitrine, 77 m hauteur totale) situé dans la forêt expérimentale H. J. Andrews à l'ouest des montagnes "Cascades" en Oregon, sont présentées. Les valeurs estimées pour la biomasse et la surface occupée par les différents composants de l'arbre sont les suivantes: tronc, 26 870 kg, 223 m²; axes (>4 cm), 1530 kg, 81 m²; brindilles vivantes (<4 cm), 480 kg, 372 m²; brindilles mortes, 78 kg, 104 m²; aiguilles, 198 kg, 2860 m²; lichens, 13.1 kg; et bryophytes, 4.7 kg. Le volume cellulaire total des microépiphytes sur les brindilles a été estimé à 300 cm³ et la couverture totale de microépiphytes sur les aiguilles a été estimée à 191 m².

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Introduction

The aboveground stems of a tree form a complex, three-dimensional surface which is the home of organisms ranging in size from bacteria, fungi, and protozoa to insects, mosses, lichens, mammals, and birds. Fundamental processes such as photosynthesis and nitrogen fixation take place on or near this surface. Whereas in terrestrial ecosystems quantities are customarily related to unit areas of the earth's surface (e.g., kilograms of biomass per square metre, number of individuals per hectare), in studying crowns of trees in a forest it is convenient to relate quantities to units of tree surface.

For several years we have been studying the role of *Lobaria oregana* (Tuck.) Müll. Arg., a nitrogen-fixing lichen which is often abundant in the crown of old-growth Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees in northwestern North America. Research on rates of nitrogen fixation by *L. oregana* and on the fates of the fixed nitrogen is in progress and is not dealt with in this paper. It is sufficient to point out that since a large variety of organisms in addition to *L. oregana* live on various surfaces of old-growth Douglas firs and since some of them may also have important roles in nitrogen fluxes within the crowns of these trees, it was desired to have a detailed knowledge of the tree and its communities of epiphytes. Although several reports of biomass analyses for Douglas fir trees have been published, they have, in general, dealt with trees less than 100 years old (Fujimori *et al.* 1976; Turner and Long 1975; Cole *et al.* 1967; Webber 1977). The few studies dealing with biomass of old-growth Douglas fir trees (Krumlik 1974; Grier and Logan, unpublished; Overton *et al.* 1973) do not present data on structure (distribution of biomass and surface area of tree components by height, size, or age) necessary for expanding estimates of quantities of epiphytes per unit of tree surface to estimates of epiphytic biomass for the entire tree.

This is primarily a methodological paper setting forth the technique developed for estimating biomass and surface area of tree components and biomass of various epiphytes, spanning the range of scale from microorganisms to the massive trunk. The trees studied are large, up to 1.5 m diameter at breast height (dbh) and 80 m in height. Results are presented from a single old-growth Douglas fir illustrating both

the sampling methodology and the structure of the crown of the tree.

An initial attempt was made to sample felled trees, but huge old-growth conifers fragment greatly when felled. Losses were especially noticeable for twigs, needles, and epiphytes, components in which we had a particular interest. Therefore we climbed and studied living trees. Some loss of tree and epiphytic components is probably inherent in any sampling scheme, but our estimates are presumed to be nearly free of the substantial bias that would have been introduced had we continued to sample felled trees.

The trees sampled are up to 450 years old and stems branching from their trunks are often a century or more old. These 'branch systems' are subject to repeated damage and subsequent growth resulting in structures varying from a single stem to multiple stems forming a fan-like pattern (Fig. 1). The branch systems also vary in mass over two orders of magnitude, from less than a kilogram to nearly 100 kilograms. Thus a large sample of branch systems would have to be obtained and processed to determine the average biomass or surface area of a branch system accurately. A sampling scheme was desired which was relatively non-destructive and which made efficient use of a small number of samples. Since our ultimate goal is estimation of stand totals, we were primarily interested in unbiased, rather than precise, estimates of biomass of components of individual trees.

The sampling method used is an outgrowth of a method suggested to us by W. S. Overton (Overton *et al.* 1973; Raj 1968; Hartley 1966; Cochran 1963). Two stages of sampling are involved. First, all units of the population are described so that predictions of the weights of various components can be made. Second, several units are selected and sampled in detail. Biomass estimates from the sampled units are expanded to tree totals with information gathered during the first sampling stage. Units subjected to detailed second-stage sampling are selected at random on the basis of a selection value (v_i) which is proportional to predicted weight²:

²The selection procedure described here is very similar to selection with probability proportional to size (*pps*) (Raj 1968). We use the term "selection value" rather than "selection probability" since by the procedure that we have used, when $x_i/X > 1/s$, $v_i > 1$.



FIG. 1. Portion of the crown of a Douglas fir tree about 20–30 m from the ground with several fan-shaped branch systems. Diameter of the trunk in the region shown is about 1 m.

$$[1] \quad v_i = s x_i / X,$$

where x_i is the predicted weight for the i th unit, s is the sample size, and X is the sum of x_i for the entire population. In its simplest form, the estimated total weight for all units of the population, $\hat{Y}$, is computed

$$[2] \quad \hat{Y} = \sum y_i / v_i,$$

where y_i is the actual weight of each of the s units sampled and $\sum$ indicates summation over the set of sampled units.

Methods

Our studies of tree biomass and structure have been carried out on watersheds 2 and 10 in the H. J. Andrews Experimental Forest 75 km east of Eugene, OR, U.S.A., in the western Cascade Mountains. The Andrews Forest is an intensive study site for both the U.S. Forest Service

and the Coniferous Forest Biome US/IBP. The trees sampled were growing between 450 and 640 m in elevation in the *Tsuga heterophylla* zone (Dyrness *et al.* 1974), where vegetation consists of an overstory of *Pseudotsuga menziesii* (Douglas fir) and *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and an understory of *Taxus brevifolia* Nutt. (western yew), *Castanopsis chrysophyllia* (Dougl.) DC. (golden chinquapin), *Rhododendron macrophyllum* G. Don (Pacific rhododendron), and *Acer circinatum* Pursh (vine maple), as well as a large variety of other species of trees and shrubs.

Data given in this report come from a tree in watershed 10 which is numbered 286 on the IBP stem map. Trees on this about 10-ha watershed were remnants of a 450-year-old Douglas fir stand with islands of younger age classes also present (Fredriksen 1972). Tree 286 (1.46 m dbh and 77 m in total height) was one of several trees selected for sampling with selection probability proportional to dbh following a scheme devised by W. S. Overton (Overton *et al.* 1973). The tree was sampled during August 1972, cut when the watershed was clear-cut in 1975, and found to be about 400 years old by counting annual rings in the stump (J. Franklin, personal communication).

Access

Trees were climbed using rock-climbing techniques described in detail elsewhere (Denison *et al.* 1972). Climbers used stirrups attached to mechanical ascenders (jumars) to climb a rope anchored to the trunk of the tree while being belayed from below. 'Spars' (3- to 5-m-long laminated beams) could be attached nearly anywhere along the trunk; they extended horizontally from the trunk when in position and enabled a sampler to move along them in a hanging seat that allowed access to most parts of very large branch systems.

Sampling Units: Definitions, Relationships, and Selection

Sampling units were chosen for convenience in the scheme outlined below and we use terms which are defined indicating their hierarchical relations as follows. The *trunk* is the main vertical axis; for epiphyte sampling its surface was divided into a series of rectangle-like *quarter sections* as illustrated in Fig. 3 and described below. A *branch system* is one or more stems which radiate from an area of a few square decimetres on the trunk. Within each branch system, stems larger than 4 cm in diameter are called *axes* and stems smaller than 4 cm are called *twigs*. Systems of twigs together with attached needles are *branchlets*.

The trunk and branch systems are sampled separately. Selection values of sampling units for both trunk and branch systems were proportional to predicted weight. Expansion of sample weights to estimates of epiphyte biomass on the trunk was done following the *pps*³ expansion method outlined by Cochran (1963). Since estimates were made of the biomass of many different branch system components, several different predictors were used, and weights of branch system components were expanded to total tree estimates using ratio expansion modified for unequal probability sampling (Raj 1968, p. 125). Note that the terms predictions and estimates are consistently used as follows: *predictions* are computed from quantita-

³Probability proportional to size.

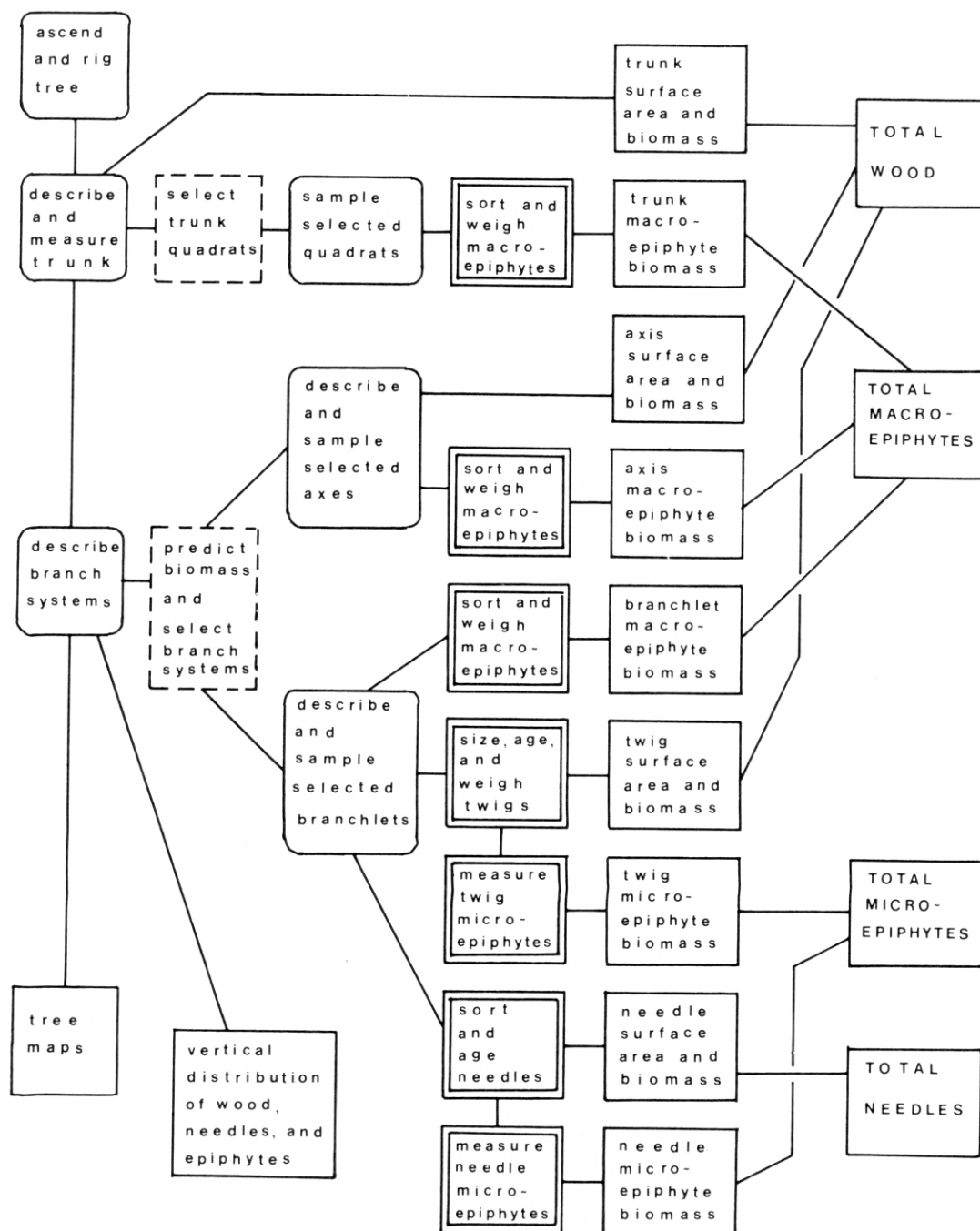


FIG. 2. Stages in description of tree structure and estimation of epiphytic biomass. Types of boxes differentiate field operations (round corners), biomass prediction and sample selection (broken lines), and laboratory operations (double lines) from output (square corners and single, solid lines). All sequences begin at upper left and proceed along connecting lines from left to right and top to bottom.

tive descriptions of a given component using relationships obtained from trees previously studied; *estimates* are computed from weights of subsamples and other measure-

ments from the tree being studied. The steps involved in making estimates of tree biomass and surface area and epiphytic biomass are summarized in Fig. 2.

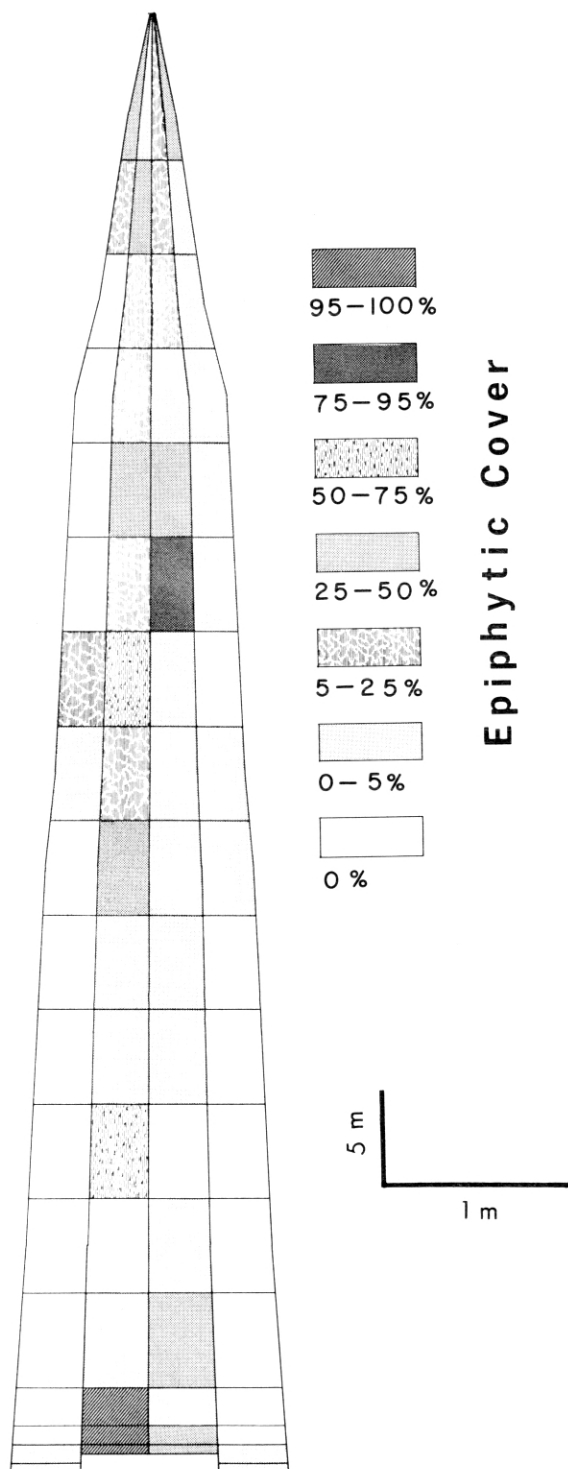


FIG. 3. Diagrammatic representation of vertical and horizontal distribution of epiphytic cover on trunk quarter sections of tree 286. The trunk surface is drawn as if it were stripped from the tree, stretched horizontally, and laid out flat. The vertical center line is the north or upper side of the trunk; the tree leans to the south.

TABLE 1. Computation of epiphytic biomass on the trunk of tree 286. The selection value, v , is proportional to predicted epiphytic biomass for the quarter section

Stratum number	Selected quarter section of trunk surface	Observed epiphyte biomass in quadrats (A), g/dm ²	Quarter section surface area (B), dm ²	Estimated epiphyte biomass on the quarter section ($\hat{y} = A \cdot B$), g	Selection value (v)	Quarter section estimates expanded to trunk strata ($\hat{y}/v$), g
1	7	0.090	114	10.2	0.1542	66
2	13	1.944	283	549.7	1.5929	345
3	13	1.944	283	549.7	1.5929	345
4	25	0.785	491	385.2	1.1080	348
5	25	0.785	491	385.2	1.1080	348
6	41	0.212	393	83.4	0.2127	392
7	45	0.443	377	166.9	0.0849	196
8	49	1.933	353	683.2	1.0849	630
9	53	0.072	334	24.0	0.4521	53
10	62	0.220	216	47.4	0.1170	405
Estimated total for trunk epiphytes = 3129 ($s_x = 539$)						

The Trunk

Trunk Description

The trunk was systematically described by measuring diameter and inclination and estimating epiphytic cover at a series of bench marks located at 5-m height intervals along the climbing path. At each bench mark, coverage was estimated within 1 dm $\times$ 2.5 dm quadrats at positions 45° and 135° around the trunk to the left and to the right of the climbing path. The primary sampling unit for epiphytes was a quarter section which we define as one-fourth of the surface of an approximately cylindrical section of trunk 5 m high, except towards the top of the trunk where sampling stopped and towards the base where epiphytic cover was expected to be relatively high and strongly stratified (Pike *et al.* 1975) and more frequent estimates were made. Quarter sections delimited by describing the trunk of tree 286 are illustrated in Fig. 3.

The weight of epiphytes on the surface of a quarter section was predicted as proportional to the product of epiphytic cover and surface area. Surface areas of quarter sections were calculated treating trunk sections as cylinders. Predicted weights of epiphytes were then converted to selection values (eq. 1). The predicted biomass of trunk epiphytes was distributed among s (in our case 10) strata each containing $1/s$ of predicted total biomass and a quarter section from each stratum was selected systematically. For purposes of illustration, quarter sections are represented by intervals of length v_i (Fig. 4) which when cumulated sum to s , and a sample is selected by the following steps. (1) Choose a random number between 0 and 1. (2) Select for sampling the unit whose interval along the axis of cumulative v_i includes the random number. (3) Select the units whose intervals include the random number plus 1, the random number plus 2, and so on to the random number plus $s - 1$. The quarter sections selected on the trunk of tree 286 contained 55.7% of the total predicted biomass of trunk epiphytes.

Sampling

The trunk quarter sections selected for epiphyte sampling on tree 286 are indicated in Fig. 4. All bryophytes and foliose and fruticose lichens were removed from a

1 dm $\times$ 2.5 dm quadrat located within the selected quarter sections at positions where the original cover estimates were made. Epiphytes were sorted into 18 taxonomic categories, air dried, and weighed. A subset of the epiphytes was oven-dried (85°C); results are corrected to oven-dry weight.

Computations

Trunk volume and surface area were computed as the sum of volumes and surface areas of a series of frusta of right cones with base and top diameters as measured at bench marks and lengths as distances between bench marks. Biomass was calculated as trunk volume multiplied by an assumed wood density of 0.45 g/cm³ (Anonymous 1952). This computed biomass is an upper limit since bark was assumed to have the same density as wood, though it is probably slightly less, and since computations assume frusta with smooth surfaces and have no correction for bark fissures. On the other hand, the surface area approximation is a lower limit since no correction was made for bark convolutions.

Weights of epiphytes were expanded to estimates for the sampled quarter sections ($\hat{y}_i$) by multiplying weights per unit of quadrat area by the computed surface area for the quarter section (Table 1). Each $\hat{y}_i$ was then divided by the corresponding selection value v_i . These quotients ($\hat{y}_i/v_i$) are, in effect, estimates of epiphytic biomass for the s sampling strata of the trunk, and $\hat{Y}$, the estimated total weight of trunk epiphytes, is, as indicated in eq. 2, the sum of these quotients for all 10 strata. Variance was approximated by the following equation which was derived from the expression for variance associated with replacement *pps* sampling (Raj 1968, p. 49).

$$[3] \quad V(\hat{Y}) = \frac{\sum_{i=1}^s (s\hat{y}_i/v_i - \sum_{i=1}^s \hat{y}_i/v_i)^2}{s-1}$$

Any sampling unit which contains more than $1/s$ of total predicted biomass not only will *always* be selected but *may* be selected more than once. Note that quarter sections 13 and 25 were both selected twice for sampling on the trunk of tree 286 (Fig. 4); weight estimates for

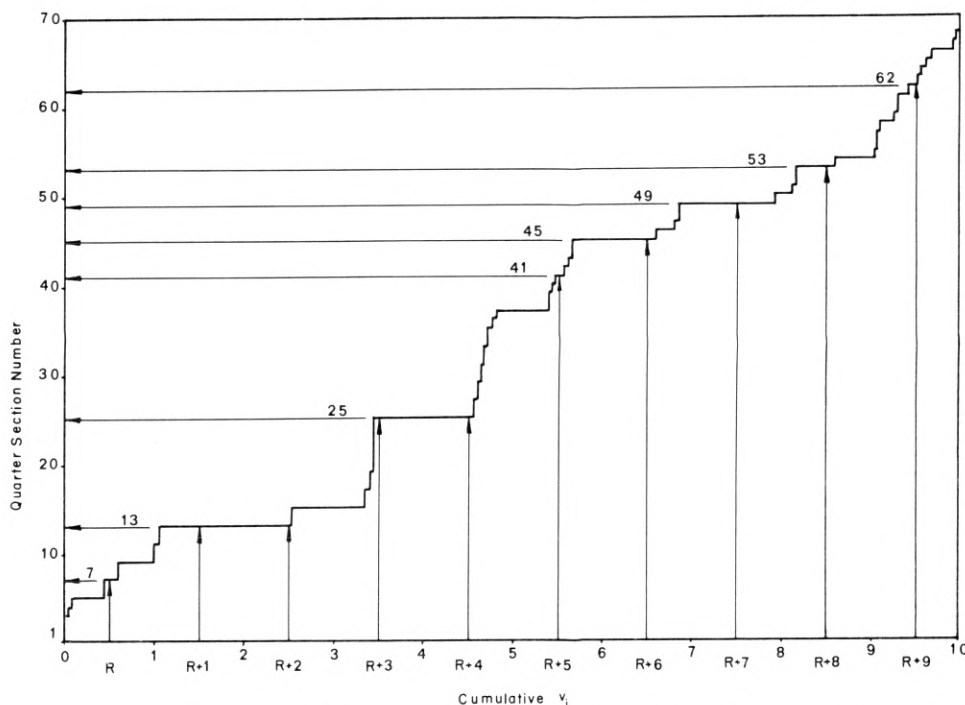


FIG. 4. Selection of quarter sections for sampling of trunk epiphytes. Each quarter section (i) is represented by a segment of line of length v_i where v_i is proportional to predicted biomass of epiphytes. The v_i s sum to 10 (the desired sample size). A systematic sample is chosen by selecting a random number (R) between 0 and 1 and including in the sample those quarter sections whose corresponding segments include: the random number; 1 plus the random number; 2 plus the random number; etc.

these quarter sections are thus entered twice in Table 1. In retrospect, a preferable procedure would have been to remove from the selection procedure any quarter sections whose $v_i \geq 1$ (Raj 1968, p. 51). Those quarter sections would have been taken into the sample with certainty and the remaining units chosen with probability proportional to predicted weight.

Branch Systems

Branch systems to be sampled were also selected with selection values proportional to predicted weight. For each branch system on the tree, measurements or estimates of several variables were made to predict biomass of tree components and epiphytes. Where estimates were made using classes (see Table 2), calculations were performed using the midpoint values of the various classes. In trees which had broken-off tops, all branch systems were described. More commonly there was a short section at the top of the tree out of safe climbing reach which was undescribed and is thus omitted from biomass estimates. We estimate that in addition to the 71 m of tree 286 that were described, 6 m of the top of the tree were not described. The 6 m of upper trunk contained about 75 living branch systems, 80% of which were <4 cm in basal diameter and thus were 'branchlets.'

Biomass and surface area of various components of each branch system were predicted using relationships (Table 3) based on geometric considerations as outlined

below and using constants empirically determined from trees sampled previously.

Axes—Biomass and surface area predictors for axes are formed from equations for volume and surface area of a frustum of a right cone.

Needles—Needle weights are found to be linearly related to branch system area (a) and to the square of axis diameter (d^2). The correlation is improved by forming a predictor which is the product of area and diameter squared ($a \cdot d^2$). However, the relationship between this predictor and needle weight is curvilinear; it is made rectilinear by taking the square root ($\sqrt{a \cdot d^2}$).

Twigs—Biomass of small twigs (<2 cm diameter) was found to be closely related to that of needles and its predictor is based on the same relationship. Biomass of large twigs was less closely related to foliage biomass than to axis diameter and thus the predictor used is a function of d^2 .

Dead twigs—Our data indicate that there are roughly two orders of magnitude more dead twigs from a dead axis than from a living axis with the same area and diameter. However, this relationship varies greatly from tree to tree, probably depending on the general health of the tree.

Macroepiphytes—A predictor of macroepiphytic biomass for branchlets was formed from estimates of area occupied by branchlet epiphytes, and a predictor of macroepiphytic biomass for axes was formed from the

TABLE 2. Information gathered for each branch system forming a set of descriptors relating to biomass and structure. Where classes are used, only upper limits are listed; the lower limit is the upper limit of the preceding class

Unit described	Descriptor	Units	Comments
Branch system	Height	m	Measured distance along trunk from the ground, ± 0.5 m
	Number of primary axes		Number of axes arising within 1 dm of trunk
	Angle of inclination	Degrees	Estimated deviation from horizontal; recorded as class values (— indicates that the system slopes down; + indicates that the system slopes up); 0, 30, 60, 90
Axes	Primary axis length	m	Estimated class: 0.1, 0.5, 1, 2, 4, 7, 10, 15
	Secondary axis length	m	Estimated total length of axes arising more than 1 dm from the trunk; recorded as classes: 0, 0.5, 1, 2, 5, 10, 15
	% alive	%	Estimated portion of total length of axes that is living; recorded as classes: 0, 5, 25, 50, 75, 95, 100
	Diameter at 1 dm	cm	Measured at 1 dm from point of attachment of axis to trunk; precision: ± 0.5 cm
	Diameter at end	cm	Estimated class: 4, 6, 8, 10, 15, 20, 25
	Total epiphytic cover	%	Estimated portion of upper surface of axes covered by epiphytes; recorded as classes: 0, 10, 40, 60, 80, 100
	Lichen cover	%	Same as above but for foliose and fruticose lichens
	Bryophytic cover	%	Same as above but for mosses and liverworts
Branchlets	Area of branch system	m ²	Area of imaginary polygon around tips of all branchlets of the branch system; recorded as classes: 1, 2, 5, 10, 15, 20, 30
	Foliage cover	%	Portion of system area covered by needles; estimated class: 0, 5, 25, 50, 75, 95, 100
	Total epiphyte area	m ²	Estimated area covered by epiphytes on all branchlets of the system; recorded as classes: 0, 0.25, 0.5, 1, 2, 4
	Lichen area	m ²	Same as above but for foliose and fruticose lichens
	Bryophyte area	m ²	Same as above but for mosses and liverworts

product of predicted axis area and estimated coverage by axis epiphytes. The form of the predicting equations and the constants have been adjusted during the course of this project as more information has become available. The relationships presented in Table 4 are those currently in use and values calculated from them are expected to approximate component biomass.

A measure of branch system size was constructed from the predicted biomasses of all its components. Since the tree and its epiphytes were of equal interest to us, selection values were proportional to a size factor which was the product of estimated tree component biomass and epiphytic biomass:

$$[4] \quad x_i = E_i(A_i + T_i + N_i),$$

where for branch system i , x_i is the size of the branch system, A_i is the predicted axis biomass, T_i is the predicted twig biomass, N_i is the predicted needle biomass, and E_i is the predicted biomass of axis and branchlet epiphytes. The number of branch systems to be sampled was five,

thus the x_i distribution was transformed to a distribution of selection values using eq. 1 with $s = 5$. The selection process was the same as that previously described for trunk sampling.

Recall that the primary sampling unit, the branch system, is made up of axes (stems > 4 cm in diameter) and branchlets (needles plus stems < 4 cm in diameter). Axes and branchlets of selected systems were described separately and subsampled to obtain estimates of biomass for individual branch systems.

Axis Sampling

The axis sampling unit was a *cylindrat*, a section of axis 1 dm long with surface area varying with diameter. Cylindrats were systematically sampled at an intensity of one cylindrat for every 5 dm of axis. Within each branch system, the location of the first cylindrat along axes from the point of attachment to the trunk was determined by choosing a random distance between 0 and 4 dm. Cylindrats were sampled on all axes within each selected branch system: all fruticose and foliose lichens and

TABLE 3. Relationships used to predict weights for various branch system components. Symbols used to form these relationships are as follows:
 α , primary axis length; β , secondary axis length; d_1 , diameter of axis at 1 dm;
 d_2 , diameter of axis at end; $c_{e,a}$, axis epiphyte cover; $c_{l,a}$, axis lichen cover;
 $c_{b,a}$, axis bryophyte cover; A_s , area of branch system; $c_{e,b}$, branchlet epiphyte
 cover; $c_{l,b}$, branchlet lichen cover; $c_{b,b}$, branchlet bryophyte cover. The
 subscripts l and $\dagger$ for axis diameters indicate living and dead axes, respectively

Component	Units	Relationship
Needle		
Biomass	kg	$0.089 \sqrt{A_s \sum d_{1,l}^2}$
Surface area	m ²	$1.24 \sqrt{A_s \sum d_{1,l}^2}$
Living twig biomass		
0-2 cm diameter	kg	$0.088 \sqrt{A_s \sum d_{1,l}^2}$
2-4 cm diameter	kg	$0.0164 (\sum d_{1,l}^2)$
Dead twig biomass		
0-4 cm diameter	kg	$0.046 \sqrt{100 A_s (\sum d_{1,\dagger}^2) + A_s (\sum d_{1,l}^2)}$
Axis		
Biomass	kg	$0.018 \alpha (d_1^2 + d_1 d_2 + d_2^2) + 1.13 \beta$
Surface area	m ²	$0.0154 (\alpha (d_1 + d_2) + 10 \beta)$
Epiphyte biomass		
Axis epiphytes	g	$c_{e,a} (0.030 \alpha (d_1 + d_2) + 0.10 \beta)$
Axis lichens	g	$c_{l,a} (0.034 \alpha (d_1 + d_2) + 0.30 \beta)$
Axis bryophytes	g	$c_{b,a} (0.014 \alpha (d_1 + d_2) + 0.12 \beta)$
Branchlet epiphytes	g	$510 c_{e,b}$
Branchlet lichens	g	$500 c_{l,b}$
Branchlet bryophytes	g	$20 c_{b,b}$

TABLE 4. Relationships used to predict weight (in grams) for various branchlet components.
 A_b = branchlet area, f = branchlet foliage cover, d = branchlet diameter, and A_e = epiphyte area

Component	Relationship used for predicting biomass in		Coefficient of determination (r^2) between observed and predicted biomass for tree 286
	Living branchlets	Dead branchlets	
Needle biomass	$19.2 \sqrt{d^2 A_b f}$	—	0.823
Living twig biomass			
< 15 years old	$10.9 \sqrt{d^2 A_b f}$	—	0.865
> 15 years old			
0-1 cm diameter	$1.8 \sqrt{d^2 A_b f}$	—	0.307
1-2 cm diameter	$7.1 \sqrt{(d^2 - 0.5) A_b f}$	—	0.851
2-3 cm diameter	$21.6 (d^2 - 3.5)$	—	0.830
3-4 cm diameter	$32.1 (d^2 - 8.5)$	—	0.837
Dead twig biomass	$2d^2$	$25d^2$	0.240
Epiphytic biomass	$8.6 A_e$	$8.6 A_e$	0.420

bryophytes were removed, the axis diameter was measured, and the cylindrat position was recorded.

Axes were approximated as a series of cylinders of diameter d and length l . Each cylinder is represented by one cylindrat in the center of which the diameter was measured (Fig. 5). Except for the beginning and end of each axis where an adjustment was made for incomplete cylinders, length of the cylinder is the same as the distance between two consecutive cylindrats (5 dm). The biomass and surface area of the axes and the biomass of their epiphytes are estimated for each branch system using the following equations:

$$[5] \quad \text{biomass of axes (kg)} = \sum_{i=1}^N 0.605 \pi (d_i/2)^2 (l_i),$$

$$[6] \quad \text{surface area of axes (m}^2\text{)} = \sum_{i=1}^N \pi d_i l_i,$$

$$[7] \quad \text{epiphyte biomass on axes (g)} = \sum_{i=1}^N w_i l_i,$$

where i is the cylindrat number, 0.605 is axis specific gravity, w_i is the weight in grams of epiphytes from cylindrat i , d_i and l_i are cylinder diameter and length, respectively, in metres, and N is the total number of cylindrats sampled within the branch system.

Branch System 31

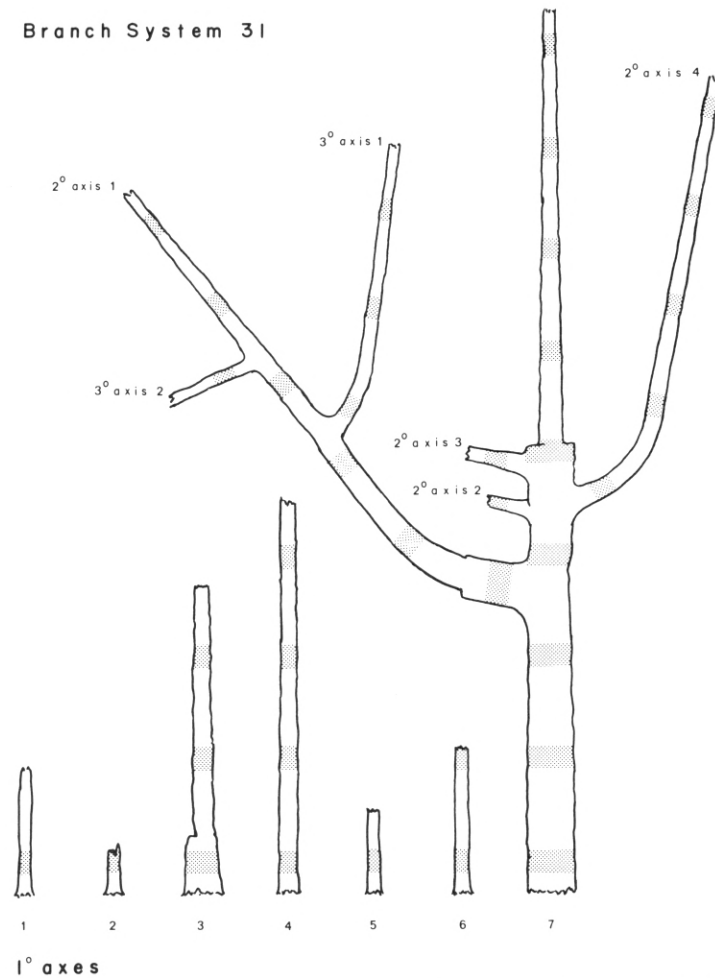


FIG. 5. Diagrammatic reconstruction of branch system 31 of tree 286 illustrating axis structure and the sampling scheme used. Primary axes arise within 1 dm of the trunk; secondary axes arise from primary axes and tertiary from secondary. Although the primary axes radiated from a small area on the trunk, we have separated them from one another for purposes of illustration. Epiphytes were removed from 1-dm cylinders (shaded) located at 5-dm intervals along the axes.

To determine axis density, a total of 15 1- to 2-dm-long sections (including bark) were removed from living axes of three trees, measured, oven-dried, and weighed. Mean density was 0.605 g/cm^3 ($s_{\bar{x}} = 0.011$). Density of dead axes was assumed to be the same as living axes.

Branchlet Sampling

Each branchlet within the selected branch systems was numbered and described (Table 5). Branchlets were sampled systematically by first ranking the branchlets by estimated area and then removing every fifth branchlet in order of decreasing size. The rank of the first branchlet removed was determined by choosing a random number between 1 and 5. Removed branchlets were cut into segments at points where their diameters were whole numbers of centimetres and sorted into diameter classes, and living and dead twigs were separated from each other.

From a subset of branchlets, living twigs were aged and cut into sections corresponding to yearly growth increments up to an age of 15 years and needles were removed. Needles and twigs produced during the growing season of 1972 (the year of sampling) are referred to as age 1 year. Epiphytes were air dried before weighing and a subset was oven-dried (85°C); all other components were oven-dried.

Since sampling probability is the same for all branchlets within a branch system, an estimate of the total weight of each branchlet component can be obtained by multiplying the average weight of the component for the sampled branchlets by the total number of branchlets in the branch system. Since branchlets vary greatly in weight, estimates based on averages have high uncertainties associated with them. However, variability in weight of various branchlet components is correlated with the

TABLE 5. Ratio estimation of the weight of branchlet components at the branch system level. The example presented here is for branch system 43, tree 286. Numbers are rounded but computations were performed on unrounded numbers

Branchlet description					Predicted biomass of branchlet components, g								
Branchlet	Diam- eter, cm	Area,* m ²	Foliage cover,* %	Epi- phyte area,* dm ²	Re- moved for analysis	Epi- phyte	Needle	Live twig <15 years	Live twig > 15 years by centimetre diameter class				Dead twig
									0-1	1-2	2-3	3-4	
1	3.0	2.00	25	5.0	No	30	273	155	26	98	119	16	18
2	3.5	2.00	0	8.0	No	56	0	0	0	0	0	0	306
3	3.5	2.00	25	0.5	Yes	2	319	181	30	115	189	120	24
4	4.0	4.00	25	5.0	Yes	30	515	292	48	188	270	241	32
5	4.0	4.00	25	8.0	No	56	515	292	48	188	270	241	32
6	1.5	0.50	0	0.5	No	2	0	0	0	0	0	0	56
7	2.5	2.00	25	0.5	No	2	228	129	21	81	59	0	12
8	4.0	4.00	50	1.0	No	6	815	462	76	296	270	241	32
9	2.5	0.25	0	2.0	No	13	0	0	0	0	0	0	156
10	1.0	0.01	0	5.0	Yes	30	0	0	0	0	0	0	25
11	2.5	1.00	25	0.5	No	2	161	91	15	57	59	0	12
12	2.0	0.50	0	5.0	No	30	0	0	0	0	0	0	100
13	4.0	4.00	25	8.0	No	56	515	292	48	188	270	241	32
Predicted total weight = $X \sum_s x_i$													
Predicted total for sample = $\sum_s x_i$													
Observed total for sample = $\sum_s y_i$													
Ratio = $\sum_s y_i / \sum_s x_i$													
Estimated total weight for branch system = $X(\sum_s y_i / \sum_s x_i)$													
						1.90	0.95	0.96	0.84	1.35	0.88	1.23	0.60
						601	3175	1820	263	1630	1323	1348	508

*These are upper limits of classes as recorded in the field; midpoints were used for computations.

quantitative information gathered during branchlet description such that the ratio of y to x is less variable than y itself. Therefore, more precise estimates of weights of branchlet components can be made using ratio estimation (Cochran 1963) than can be made based on averages. The total weight of a given branchlet component within a particular branch system is estimated by

$$[8] \quad \hat{Y} = X \frac{\sum_{i=1}^s y_i}{\sum_{i=1}^s x_i},$$

where for the i th branchlet, x_i and y_i are, respectively, the predicted and observed weights of the component, X is the sum of the predicted weights of the component for all branchlets within the branch system, and $\sum$ indicates summation over the set of sampled branchlets.

A set of relationships (Table 4) was developed to predict weights of components of branchlets based on their descriptions. The predictors correlated well with observed weights of branchlets, although for any given tree the r^2 s between predicted and observed weight were quite low for some branchlet components. The relationships used to predict weights are presented in Table 5 along with r^2 values for components from tree 286. Computations of estimated weights for branchlet components of branch system 43 are shown in Table 5 as an example.

Expansion to Total Tree

Methods used for computing tree totals for axis and branchlet components parallel those used for estimating branch system totals for branchlet components. However, since branch systems were selected with selection values proportional to predicted weight, observed and predicted values of sampled branch systems are weighted by v_i when total tree estimates are being made. Thus the expansion formula becomes

$$[9] \quad \hat{Y} = X \frac{\sum_{i=1}^s \hat{y}_i / v_i}{\sum_{i=1}^s x_i / v_i},$$

where for the i th branch system, x_i is the predicted component weight, $\hat{y}_i$ is the estimated component weight, and v_i is the selection value. X is the sum of predicted component weight for all branch systems on the tree, and s is the set of sampled branch systems. The derivation of eq. 9, which we call modified ratio estimation, is discussed by Raj (1968, p. 125).

For any branch system component, the modified ratio is constructed from the predicted weight or surface area and the estimated weight or surface area for that component. The estimates are obtained from axis or branchlet sampling. The set of predictive relationships developed for branch system components was discussed earlier (cf. Table 2). Coefficients of determination between estimated and predicted branch system biomass of tree 286 are found in Table 8. Standard errors for branch system components were approximated following the same approach as that used for trunk epiphytes (eq. 3).

Twigs, Needles, and Microepiphytes

Estimates of age-specific distribution of needle and twig biomass and surface area for entire trees were made by first determining the age-specific distributions of weight

and the surface-area-to-weight ratios for twigs and needles in a branchlet selected from those removed from each branch system. This branchlet was assumed to be representative of the entire branch system and age distribution and surface area data were used to transform total biomass estimates computed by eq. 8 to age-specific biomass and surface area estimates for the branch system. Branch system estimates were expanded to total tree estimates by eq. 9.

Estimates of microepiphytic cover were made for twigs and needles of several ages from several heights in the canopy. Since there appeared to be little consistent variation with height and since neither all ages of twigs and needles nor all heights in the canopy were sampled, average age-specific coverage values for microepiphytes were applied to total tree estimates of twig and needle surface area.

Methods for determining age distribution and biomass of twigs and needles and for estimating microepiphytic cover are discussed briefly below.

Twig and Needle Age Distribution

For representative branchlets, twigs were aged up to a maximum age of 15 years. In determining the ages of the twigs, we relied largely on branching pattern and positions of terminal bud scars. Since some buds may fail to grow in any given year, difficulties were encountered in aging twigs. Size and orientation of needles produced in specific years were observed to vary in consistent patterns helpful in assigning ages. We found, for example, that needles produced in 'cone years' were noticeably shorter than those produced in non-cone years; this effect was particularly pronounced in the upper portion of the canopy. Needles were removed from the twigs and separate needle and twig weights were recorded for each age class.

Needle Surface Area

Length (L) and width (W) were measured for six randomly selected needles for each age and each representative branchlet. Surface area for these needles was computed by multiplying the product LW by a constant, K , equal to 2.12 (Barker 1968). The surface-area-to-weight ratio for a sample of six needles was determined by dividing total computed surface area by total oven-dry weight of the needles.

Barker (1968) determined that K varied little from 2.12 for Douglas fir trees of various ages in British Columbia. We determined the value of this constant for samples of six needles from each of three age classes (1, 3, and 5 years) and each of three heights in each of three trees sampled in the early months of 1976. Our methods were essentially the same as those described by Barker. Our values of K were generally within 2% of Barker's value and analysis of variance failed to show significant variation with age of needle, height in canopy, or tree from which the needles were taken.

Twig Surface Area

Surface-area-to-weight ratios were determined for twigs of ages 1 through 15 years and for diameter classes of twigs older than 15 years. Length and diameter of all (or a large subsample) of twig segments were measured from representative branchlets. The surface-area-to-weight ratio for a sample of twigs was determined by dividing total computed surface area by total dry weight of the twigs.

Twig Microepiphytes

Microepiphytes were removed from cylindrats located at random positions along segments of living twigs. One cylindrat was sampled for one segment of each of nine ages selected randomly with probability proportional to quantity of microepiphytes expected, where the expected amount was based on relationships found in preliminary sampling on other Douglas fir trees from watershed 10. Edges of the cylindrat were scored by turning the twig against two razor blades mounted 3.3 mm apart in a wooden block. The surface of the cylindrat was moistened with water, and microepiphytes were scraped off using a flattened probe. Care was taken not to dislodge any but a thin outer layer of bark cells. Microepiphytes were dispersed in a drop of alkaline mounting medium (equal parts of 10% aqueous KOH and glycerin) and covered by a 22×22 mm cover slip.

All fungal and algal cells found in 40 microscope fields (at $1000\times$) were counted and identified either to species or larger taxonomic group. No attempt was made to distinguish between dead and living cells. Fields were spaced at equal intervals along a transect running vertically, horizontally, or along either diagonal of the cover slip. To compensate for the uneven distribution of microorganisms under the cover slip, counts from each field were multiplied by a factor directly related to the distance of each field from the centre of the cover slip.

Cell counts were converted to estimates of total cell volume by multiplying numbers of mean cell volume. Cell volumes were determined by measuring diameter or long and short axes of about 100 cells of each taxon. Mean volumes are means of volumes computed separately for each cell measured; the shape of each cell was approximated as a sphere, cylinder, or ellipse rotated about its long axis as deemed appropriate.

Needle Microepiphytes

Coverage estimates for needle microepiphytes were made by M. A. Bernstein using fluorescence microscopy; techniques have been described elsewhere (Bernstein *et al.* 1973; Bernstein 1974) and are not discussed here. Values of microepiphytic cover for top and bottom surfaces of 1-, 3-, 5-, and 8-year-old needles are taken from Table 5 of Bernstein (1974). These values were averaged for various canopy heights and values for intermediate ages were interpolated.

Results

The description, sampling, and analyses outlined above yield several different kinds of information about individual trees. Some information is spatial and best expressed as maps or diagrams. Some provides estimates of total amounts of specific components for the entire tree, for example, axis biomass or foliage surface area. Some relates the distribution of specific epiphytes or classes of epiphytes to parts of the tree. Some, such as age-specific estimates of needle, twig, and microepiphytic cover, is temporal. Each of these types of information is presented separately below.

Maps

From the initial description of the trunk and branch systems it is possible to map the structure of the tree. It takes two maps to display the whole tree; one drawn in the north-south plane depicts the branches projecting to the north and south (Fig. 6); the other drawn in the east-west plane depicts the branches projecting to the east and west (not illustrated).

The trunk is drawn to scale, usually 1:100 on the original, with the diameter and inclination from the vertical taken from measurements at each bench mark. In the example shown, the trunk leans consistently to the south, but it wanders back and forth in the east-west plane. This particular tree grew on a steep, south-facing slope. As is usually the case, it leaned away from the slope.

Each branch system is represented by one or more solid or broken lines, with or without a rectangle representing foliage. The branch systems are spaced along the trunk using the vertical scale of the trunk, but the branch systems themselves are drawn to a different scale. The internal structure of most branch systems is too complex to draw. Furthermore, we did not record patterns of secondary and tertiary branching except in those branch systems which were sampled in detail. Therefore the diagrams of individual branch systems are graphic representations of the values of five variables, namely: lengths of living (solid lines) and dead (broken lines) primary axes; branch system area ('foliage' boxes); and two angles, the angle between the first metre of the branch system and the trunk, and the angle which the whole branch system, from base to tip, makes with the horizontal.

In general, the scales are selected to provide an apparent crown diameter which has the same scale as trunk diameter.

The tree maps serve functions similar to those of conventional geographic maps. They serve, for example, to locate different types of habitat, e.g., living versus dead branch systems, or long stretches of exposed trunk, within the crown. They facilitate communication among experimenters working on the same tree and aid in planning the placement of instruments or establishment of long-range study sites.

Vertical and Horizontal Distributions

Our sampling was designed to yield relatively

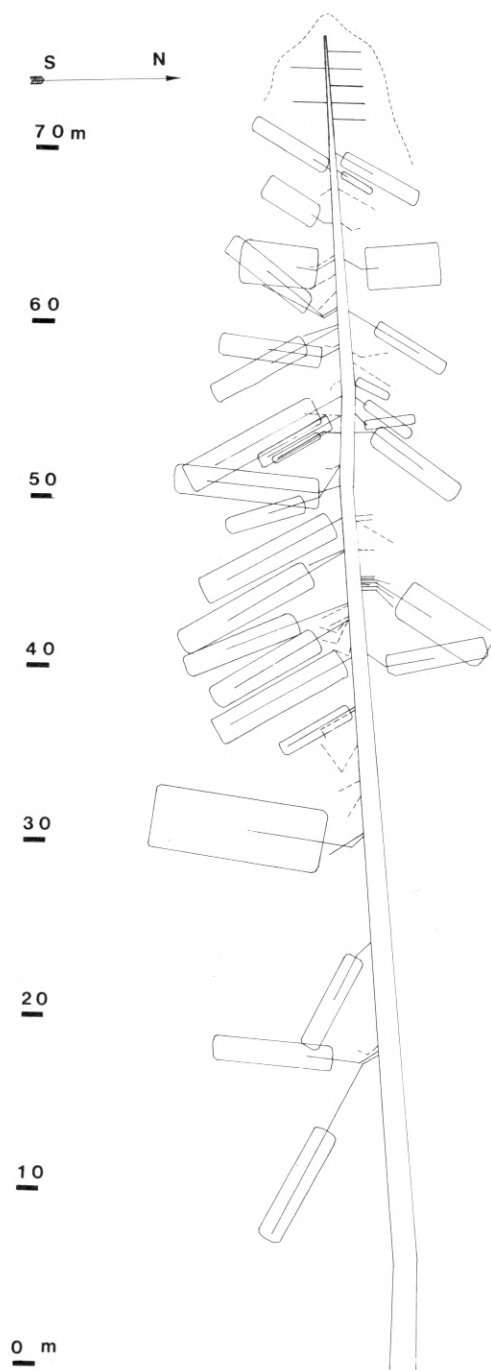


FIG. 6. Map of tree 286 in the N-S plane. The trunk is drawn to scale, branch systems are not. Within branch systems, solid lines represent living axes and broken lines represent dead axes. Living branch systems have a rectangular 'foliage box' whose length is proportional to branch system area and whose width is proportional to

precise and unbiased whole-tree estimates for various components and was not designed to analyze the within-tree distributions of biomass and surface area. However, since there is generally a good correlation between predicted and observed biomass at the branch system level and since the ratios between observed and predicted biomass are similar from branch system to branch system and from tree to tree, we feel that our biomass predictions accurately reflect patterns of distribution of biomass and surface area for various components. We have analyzed vertical and horizontal distribution for branch systems aggregated into 5-m-high strata starting with the bench mark at which the first branch system occurs (Table 6). This aggregation minimizes artifacts owing to imprecision in describing individual branch systems.

Roughly half of the total branch system biomass for tree 286 is found below 50 m (Table 6). However, many more branch systems were found above 50 m, indicating that their average size is much smaller than branch systems found in the lower part of the crown. The concentration of large branch systems in the lower part of the crown is also reflected in a center of distribution of axis biomass which is lower than that found for needle and twig biomass. The similar vertical distributions of needle and living twig biomasses are expected because of the biological relationship between twigs and needles; however, these distributions are mathematically related because of the close similarity between the predictive relationships used (Table 3).

The vertical and horizontal distribution of axis lichen biomass is similar to the distribution of axis biomass and surface area (Table 6 and Fig. 7), whereas axis bryophytes are abundant in the lower half of the crown and almost absent from the upper half (Fig. 8). The same pattern is found for branchlet epiphytes: the distribution of lichens is similar to that of twigs and needles, whereas bryophytes are found only in the lower half of the crown (Table 6).

Biomass of Tree Components

About 92% of the estimated biomass for tree 286 was in the trunk (Table 7). Axes and twigs

the percentage of branch system area that is covered by foliage. Slopes of axis lines and foliage boxes represent angles made by the first metre of axis and the rest of the branch system with the horizontal.

TABLE 6. Vertical distribution of biomass of needles, twigs, axes, and epiphytes on branch systems of tree 286. Values are percentages of tree totals predicted for each 5-m-high stratum

Stratum	Height, m	Needles	Living twigs	Axes	Axis lichens	Axis bryophytes	Branchlet lichens	Branchlet bryophytes
1	14.5-19.5	4.9	4.9	5.2	5.0	9.9	3.4	20
2	19.5-24.5	0	0	0	0	0	0	0
3	24.5-29.5	4.4	4.8	5.4	1.8	10.4	1.7	20
4	29.5-34.5	7.7	8.0	6.8	3.7	13.3	6.0	30
5	34.5-39.5	4.3	4.7	6.4	3.4	3.4	5.1	10
6	39.5-44.5	9.4	10.1	18.1	11.7	24.5	11.1	10
7	44.5-49.5	11.0	11.1	10.0	10.9	21.2	6.0	10
8	49.5-54.5	14.3	13.9	14.8	16.1	10.7	12.8	0
9	54.5-59.5	17.5	17.2	15.8	17.6	5.2	18.8	0
10	59.5-64.5	12.3	11.7	8.3	11.9	1.0	13.7	0
11	64.5-69.5	11.6	11.1	7.8	15.2	0.5	14.5	0
12	69.5-71.5*	2.7	2.6	1.2	2.7	0.0	6.8	0

*No predictions are included for the top of the tree (between 71.5 m and 77 m) since branch systems were not described above the level which climbers could sample.

TABLE 7. Estimated biomass (ovendry weight) and surface area of tree 286. The coefficient of determination (r^2) is that between predicted and estimated biomass of branch system components, and the sampling intensity is the percentage of total biomass predicted for the sampled branch systems

Component	Biomass $\pm s_{\bar{x}}$,* kg	Surface area $\pm s_{\bar{x}}$,* m ²	r^2	Sampling intensity
Needles	197.8 $\pm$ 40.7	2816.4 $\pm$ 642.4	0.984	12.0
Living twigs				
<15 years old	118.5 $\pm$ 26.6	253.2 $\pm$ 55.7	0.988	12.0
>15 years old				
0-1 cm diameter	30.7 $\pm$ 12.5	23.4 $\pm$ 10.5	0.580	12.0
1-2 cm diameter	131.1 $\pm$ 43.4	49.9 $\pm$ 17.4	0.769	12.0
2-3 cm diameter	92.5 $\pm$ 32.2	25.0 $\pm$ 9.2	0.842	11.9
3-4 cm diameter	106.0 $\pm$ 29.1	21.4 $\pm$ 5.8	0.786	11.9
Dead twigs				
0-4 cm diameter	77.8 $\pm$ 12.8	104.0 $\pm$ 18.4	0.956	9.4
Axes				
(>4 cm diameter)	1530.8 $\pm$ 183.4†	81.4 $\pm$ 10.1†	0.991	10.4
Trunk	26 871.3	222.9	—	—
Total	29 156.4	3597.6	—	—

*Standard error of the mean = $s_{\bar{x}}$.

†Living axes account for 1284.4 kg and 68.3 m² of the estimated total weight and surface area of axes, respectively.

account for 5% and 2%, respectively, of the total biomass, and needles account for less than 1%. In contrast, needle surface area was 78% of total surface area, with twigs, trunk, and axes accounting for 13%, 6%, and 2%, respectively. One surprising result is the 78 kg biomass estimate for dead twigs: their biomass is nearly one-third that of the needles.

Biomass of Macroepiphytes

Biomass of the lichen *Lobaria oregana* is more

than half of the total estimated macroepiphytic biomass for tree 286 (Table 8). *Lobaria* and other lichens account for nearly three-fourths of the total epiphytic biomass with virtually all of the remainder contributed by mosses. Data from the first tree sampled quantitatively (later numbered 1109; Pike *et al.* 1972) indicated that a substantial portion of epiphytic biomass occurred on branchlets. Branchlets were sampled more intensively on tree 286 than they were on tree 1109, and nearly half of the total epiphytic biomass and 70% of

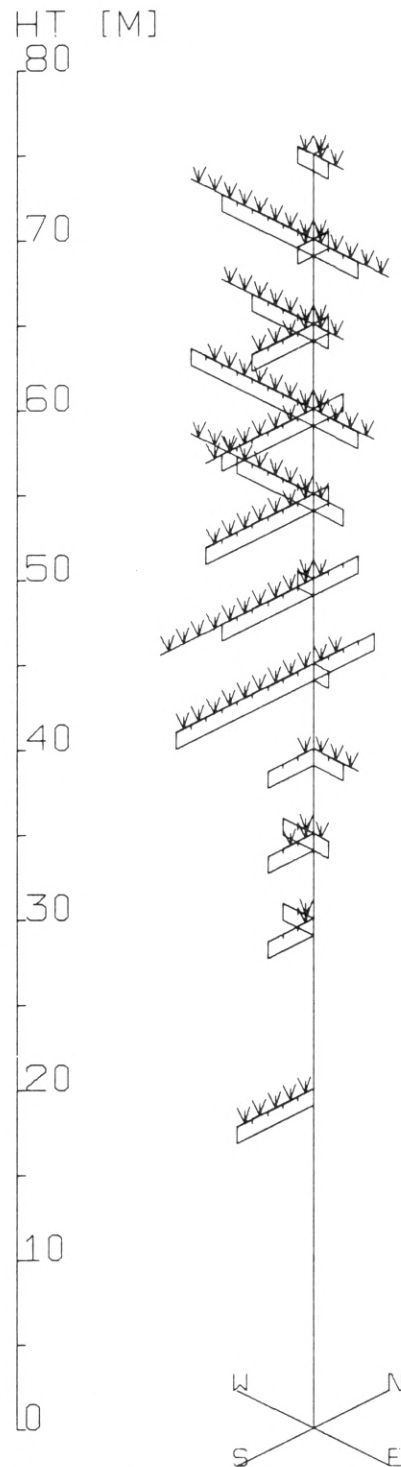


FIG. 7. Horizontal and vertical distribution of predicted biomass of axis lichens in relation to predicted axis

the *Lobaria* biomass were found on branchlets.

Age Distribution of Needles and Twigs

We estimate that there were about 10 to 12 million needles on twigs of each age from 1 to 3 years (Table 9); each of these age classes of needles had total surface areas of 500–600 m². Needle number and surface are both decreased to half of the initial value between ages 5 and 6 years. Average needle weight increased with age, however, so that total needle weight did not decrease to half of its initial value until about age 7 years.

Total twig length for each age from 1 to 3 years was estimated to be 6–7 km; half of the initial value is reached between ages 7 and 8 years (Table 9). As twigs fall off, those remaining increase in diameter so that total twig surface area for each age remains relatively constant between ages 1 and 6. Twig biomass remains relatively constant, with values of 6–7 kg for each age, except for a broad peak centered on ages 5–6 years where biomass increases to about 10 kg.

Our data indicate that about half (51.7%) of the needle biomass on tree 286 was less than 3 years old (Table 9). We found that there were more 2nd- and 3rd-year needles than 1st-year needles. Since sampling took place during August, it seems unlikely that 1st-year needles were still being produced. Although it is possible that lower numbers of needles were produced in 1972 than were produced in 1971 and 1970, the data suggest that some of the needles were not correctly aged. First-year needles were easily recognized; where buds did not burst, it was obvious that terminal needles were older than 1 year. However, where a bud failed to burst in some past year, twig segments and attached needles may have been incorrectly assigned to an age class 1 year too young. Thus the fraction of needles estimated to be in young age classes (but older than 1 year!) may be too high. Overton *et al.* (1973) have aged and weighed needle samples from old-growth Douglas fir tree 174 also on watershed 10 of the H. J. Andrews

surface area. Branch systems are aggregated within 5-m-high strata. Lengths of bars are proportional to total axis biomass: ticks divide bars into sections, each of which corresponds to 1% of predicted tree total. Each tuft on the bars corresponds to 1% of the biomass of axis lichens predicted for the tree.

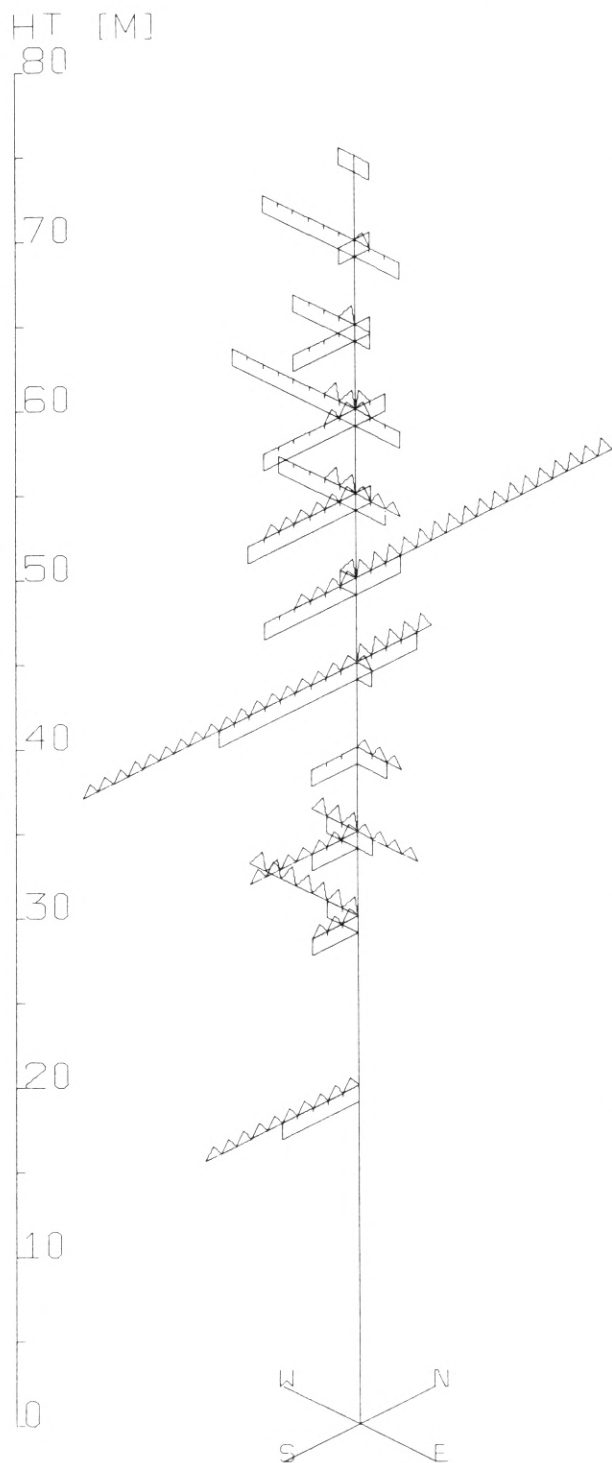


FIG. 8. Horizontal and vertical distribution of predicted biomass of axis bryophytes in relation to predicted

Experimental Forest. Although their estimate that 40.1% of needle weight is 3 years old or less is lower than the 51.7% which we report here for tree 286, it is close to the 37.9% figure independently obtained for tree 174 (Pike, Denison, Carroll, and Rydell, unpublished data).

Age Distribution of Microepiphytic Cover

Total microepiphytic cover on needles has increased by age 3 to a value of about 30 m² (Table 9); this value is sustained until year 5 after which decreasing needle surface area results in a rapid decrease for older classes of needles. Microepiphytic cover on individual needles increased as long as the needle remained on the tree.

Microepiphytic cell volume on twigs increased from a value of 0 at age 1 to a value of 30 to 35 cm³ which held from 5 to 9 years (Table 9). Cell volume then dropped to about 13 cm³ by 13 to 15 years. The 300 cm³ estimated as the total cell volume of twig microepiphytes is a conservative estimate since estimates are not included for dead twigs or for twigs older than 15 years.

Studies are being carried out by Dr. George Carroll, a colleague, which will result in estimates of the average thickness of the layer of microepiphytes on needles and in estimates of dry weight per unit of cell volume of microepiphytes. We do not, at present, have a basis for converting these estimates of cover and cell volume to estimates of biomass.

Discussion

We have used the basic methods described in this paper to sample nine old-growth Douglas fir trees (dbh = 1.07 to 1.80 m, height = 50 to 77 m); several others were partially sampled during development of methods. In addition, we have sampled one large hemlock (dbh = 0.45 m, height = 28 m), one large sugar pine (dbh = 1.15 m, height = 55 m), and nine smaller, understory trees (dbh = 0.18 to 0.30 m, height = 8 to 17 m). With minor modifications, the sampling methods have proved satisfactory for the variety

axis surface area. Branch systems are aggregated within 5-m-high strata. Lengths of bars are proportional to total axis biomass: ties divide bars into sections, each of which corresponds to 1% of predicted tree total. Each upright tooth on the bars corresponds to 1% of the biomass of axis bryophytes predicted for the tree.

TABLE 8. Estimated biomass (kilograms of oven-dry weight) $\pm$ standard error for epiphytes on trunk, axes, and branchlets of tree 286

Epiphyte	Trunk	Axes	Branchlets	Total
Lichens				
<i>Lobaria oregana</i>	0.00	3.13 $\pm$ 2.35	7.08 $\pm$ 7.18	10.21 $\pm$ 9.53
Other cyanophiles*	0.00	0.02 $\pm$ 0.007	0.01 $\pm$ 0.02	0.03 $\pm$ 0.03
Non-cyanophiles†	0.64 $\pm$ 0.09	0.72 $\pm$ 0.36	1.52 $\pm$ 1.41	2.88 $\pm$ 1.83
Bryophytes				
Mosses	2.49 $\pm$ 0.13	2.06 $\pm$ 1.39	0.03 $\pm$ 0.04	4.57 $\pm$ 1.58
Liverworts	0.00	0.07 $\pm$ 0.07	0.03 $\pm$ 0.04	0.10 $\pm$ 0.11
Total	3.12 $\pm$ 0.13	6.00 $\pm$ 1.74	8.67 $\pm$ 6.93	17.79 $\pm$ 8.80

*Cyanophilic lichens (containing a blue-green alga as either a primary or a secondary phycobiont and thus capable of fixing atmospheric nitrogen) include genera such as *Lobaria*, *Pseudocyphellaria*, *Peltigera*, and *Nephroma*.

†Non-cyanophilic lichens (containing a green alga as the only phycobiont and thus incapable of fixing atmospheric nitrogen) include genera such as *Hypogymnia*, *Platismatia*, *Alectoria*, and *Sphaerophorus*.

TABLE 9. Age-specific distribution of needle and living twig biomass, surface area, number (or length), and microepiphyte cover for tree 286

Age, years	Needle				Twig			
	Biomass, kg	Surface area, m ²	Number, millions	Microepiphyte cover, m ²	Biomass, kg	Surface area, m ²	Length, km	Microepiphyte cell volume, cm ³
1	29.4	482	9.96	6.6	6.0	22.7	6.33	0.0
2	40.9	615	12.25	25.2	7.5	28.9	7.45	3.2
3	31.9	480	12.64	29.8	8.4	25.1	6.73	5.5
4	27.3	384	7.79	30.7	8.9	27.8	6.45	28.8
5	22.8	305	6.18	29.1	10.5	29.6	6.40	37.4
6	18.1	216	4.55	24.2	9.6	24.9	4.83	29.6
7	16.4	208	3.87	26.6	8.9	20.9	3.80	35.9
8	6.9	83	1.74	11.8	8.4	16.9	2.89	34.2
9	3.6	42	0.77	6.4	8.5	14.8	2.22	30.6
10	0.2	2	0.04	0.3	7.3	10.6	1.30	23.1
11					6.7	8.1	0.80	18.3
12					6.1	6.4	0.53	14.1
13					7.4	6.5	0.45	13.5
14					7.4	5.6	0.32	13.4
15					6.7	4.4	0.22	12.9
Total	197.8	2816	60.67	190.9	118.5	253.2	50.72	300.5

of trees studied. Once the basic tree structure was reconstructed, analysis of age distributions, epiphyte data, and vertical distributions was relatively straightforward. After a tree has been described and sampled, it is possible to devise sampling schemes for additional crown components as long as they can be related to the structure of the tree.

Although the branch systems selected for detailed analysis contained 10 to 12% of the predicted branch system biomass of these trees (Table 7), the proportion of total branch system biomass removed from the tree was generally

small, for example, about 2% of all components except for the trunk and axes was removed from tree 286. Thus our sampling has been relatively non-destructive, allowing several of these trees to be used for long-term studies.

Since axis biomass is the major component of branch system biomass and since axis biomass varies over more orders of magnitude than does epiphyte biomass, selection values (v_i , eq. 4) are more closely related to predicted axis biomass than they are to predictions for other components. Since our method of computing variances depends upon the relationship between

observed weights and v_i , those components whose predicted biomass have high correlations with the v_i s are likely to have relatively small error bounds (Table 7). Those components (epiphytes in particular) which did not correlate well with axis biomass have correspondingly large error bounds (Table 8).

Although the climbing techniques used allowed access to most of the canopy, the top of some trees remained inaccessible. For tree 286, this leads to an underestimate, which we have not attempted to correct, for certain components. Since the climbing path stopped a few metres from the top of the tree, most of the undescribed branch systems were young, healthy, and had no axis. Thus the axis and dead twig estimates are only slightly affected by this omission; the tree components whose estimates are most affected are twigs and needles. The epiphytic species which were abundant on branchlets in the exposed, upper portions of the crown (*Alectoria sarmentosa*, *Platismatia* spp., *Hypogymnia* spp.) may have been significantly underestimated while estimates for the more mesophytic epiphytes (bryophytes, *Lobaria oregana*, *Sphaerophorus globosus*) were less affected.

Valentine and Hilton (1977) have recently described a method for sampling foliage on oak trees that is similar in some respects to the method that we have described: sampling involves two stages and selection probabilities are unequal and are based on predictions of quantities present. Our sampling schemes differ in part because of differing objectives and structure of the trees sampled. Whereas we have developed predictors for several different tree and epiphyte components, Valentine and Hilton sampled only foliage. By our selection procedure, the probability of selecting a given branch system depended upon the distribution of weights predicted from a complete inventory and description of branch systems. By the selection procedure followed by Valentine and Hilton, the probability of selecting any given foliage cluster was the product of the series of probabilities of making the necessary choice of route at each dichotomy met as the sampler moved along the branch. Although our sampling method works well on conifers where branch systems arise from the trunk as discrete entities, we suspect that it cannot be easily adapted for use on many angiosperms where branching occurs more or less throughout the tree.

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