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Title: ROOT BIOMASS STUDIES OF OLD-GROWTH DOUGLAS-FIR

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Root biomass studies were conducted in an old-growth stand of conifers in the western Cascades of Oregon. The root systems of three Douglas-firs (Pseudotsuga menziesii var. menziesii (Mirb.) Franco) with diameters at breast height of 94, 110, and 135 cm were excavated and weighed to provide a basis for regression equations for estimating the biomass of roots larger than 10 mm in diameter in the stand. The biomass of small roots was estimated from soil core samples taken within the stand. The total root biomass in the stand sampled was estimated as 210 t/ha. The contribution of small roots to this total amount was estimated as 11.3 t/ha.

Nutrient analyses were performed on root samples from both the excavated root systems and the soil cores. Results were used for projecting the nutrient capital contained in the roots of the old-growth stand.

Data from previous investigations of root biomass were compared

with results of the present study. A double logarithmic plot of root system biomass on stem diameter at breast height shows a linear relationship. Closer examination suggests that the variation in the root system biomass to diameter relationship within a given species is comparable to the variation between different species. Fine root biomass, estimated as 9.7 t/ha, falls within the range of values found by other investigators.

Root Biomass Studies of Old-growth Douglas-fir

by

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ROOT BIOMASS STUDIES OF OLD-GROWTH DOUGLAS-FIR

INTRODUCTION

Biomass studies are fundamental to understanding the dynamics of ecological systems. Estimations of biomass are essential in determining the distribution and flow of materials in ecosystems, necessary to understand the dynamics of these systems (Andersson 1971). However, biomass determinations are only static, descriptive studies, dealing with how much living material is contained in a given space or system at a particular time. These studies are comparable to viewing one frame of a motion picture. Only when the dimension of time is added may the system be viewed in motion as a dynamic one. Accordingly, dynamic studies deal with the system in motion, as it functions or is affected by change. Just as the story of a motion picture is told through a series of still frames, dynamic studies often consist of a series of static studies performed over an interval of time. Dynamic aspects such as growth, productivity, turnover, etc. may be characterized by monitoring the changes in biomass over intervals of time. In this manner, biomass studies may be employed to quantitatively describe the static state of ecological systems, and may also be repeated in sequences to study various dynamic aspects of these systems.

The last 20 years have brought an emergence of ecosystem studies. This growing interest in the dynamics and productivity of ecosystems has pointed out the need and has led to attempts for a better understanding of roots as a part of the entire system. However, progress in understanding the belowground portions of ecosystems has lagged. W. F. Harris (1971) states,

> Although the importance of roots as structural, storage, and physiologically active organs has been known, they have been neglected for the most part in 'ecosystem studies' to date because of difficulties surrounding their study.

Studies involving roots inherently must cope with some difficult problems, the most obvious being the overburden of the soil. This overburden makes these systems invisible; observation is not possible without a great deal of effort and disturbance. Moreover, the soil is generally the environment of the roots; its removal constitutes such a drastic change that subsequent observation is likely to give an atypical picture. Recognizing these limitations, most investigations of roots are still exploratory by nature. The approach presented herein provides a flexible structure for performing static and dynamic studies on the belowground portions of ecosystems.

The present investigation was carried out as a part of an integrated study by the U. S. International Biological Program in an effort to analyze and model coniferous forest ecosystems. The forest ecosystem has been divided into five major compartments: the canopy layer, the subordinate vegetation layer, the forest floor layer, the rooting zone layer, and the subsoil. A major objective of the modeling effort has been to quantify descriptive and dynamic aspects of biomass, productivity, and the flux of materials for each compartment. The principal objective of this study was to quantitatively describe the total root biomass contained within the rooting zone layer of an old-growth stand of Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco). At the same time, it was desirable to sample in a manner that would yield data amenable to analyzing the spatial distribution of root biomass around individual trees as well as between different plant communities within a small watershed in the central portion of the western Cascade Mountains. This paper contains the results of this study, and comparisons and evaluations of these results with respect to the findings of previous investigations of root biomass.

LITERATURE REVIEW

Historically, three phases can be distinguished in the study of tree roots. Nearly all early investigations were confined to anatomical and morphological descriptions of roots. Gradually, investigators shifted their efforts toward studies of the ecological and physiological factors affecting root growth and distribution. Many of the papers pertaining to these two phases have been reviewed by Karizumi and Tsutsumi (1958), Köstler et al. (1968), Lyr and Hoffmann (1967), Röhrig (1966), Sutton (1969), and Weller (1965). The growing interest during the last 20 years in the dynamics and productivity of forest ecosystems has pointed out the need of, and has led to attempts for, a better understanding of roots as a part of the entire system. The relatively few studies in this latest phase of root investigations have been summarized by Ovington (1962) and in papers presented at the 1968 symposium "Methods of Productivity Studies in Root Systems and Rhizosphere Organisms" in the Soviet Union (USSR Academy of Sciences 1968) and at the 1969 Brussels symposium "Productivity of Forest Ecosystems" (UNESCO 1971).

Systematic investigations of root biomass were begun only during the last two decades. Information on a number of these investigations is presented in Table 1. Published data indicate that root biomass studies have been conducted mostly on trees less than 100 years old.

Table 1. Root Biomass in Conifer Forests.

Reference	Country	Status	Age		DBH		Height		Sample size	Tree basis: Root biomass			Stand basis			
			Range (yr)	Avg. (yr)	Range (cm)	Avg. (cm)	Range (m)	Avg. (m)		Range (kg)	Avg. (kg)	% of total biomass	Density (no/ha)	Root biomass (t/ha)	Shoot biomass (t/ha)	Roots as % of total biomass
Abies balsamea																
1	Canada	Natural		42	2-25		2-15		89	0.2-53						
2	Canada	Natural		43		8		8	18				12,300	46	154	23
"	"	"		43		10		10	19				7,400	41	142	22
"	"	"		"		11		10	19				4,900	38	129	23
"	"	"		"		11		9	12				3,600	36	113	24
"	"	"		"		12		10	13				2,800	30	103	23
"	"	"		"		14		11	18				1,700	30	107	22
3a	Canada	Natural	8-45	25	1-40	14	2-19	9	40	0.2-142	24	20				
3b	"	"	50-70	58	10-33	19	12-23	17	40	3.8-72	26	17				
Cryptomeria japonica																
4	Japan	Plantation		24		17		13	10		17		1,750			
Picea abies																
5	USSR	-		120		15		11	10					11	40	22
6	USSR	-		200	35-40			31	20					85	255	25
7	Sweden	Plantation		55	15-38	28	18-28	25	3		65	15	800	59	308	16
8	USSR	-		130		17		18	10					66	131	34
"	"	-		110		20		19	20					77	197	28
9	USSR	-		72		18								65	226	22
"	"	-		83		26								78	280	22
"	"	-	45-55			19								33	198	14
10	USSR	-		125		24		15	11					41	133	24
11	USSR	-		24										20	72	22
"	"	-		38										38	123	24
"	"	-		60										65	217	23
"	"	-		93										65	260	20

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Table 1. (Continued)

Reference	Country	Status	Age		DBH		Height		Sample size	Tree basis: Root biomass			Stand basis			
			Range (yr)	Avg. (yr)	Range (cm)	Avg. (cm)	Range (m)	Avg. (m)		Range (kg)	Avg. (kg)	% of total biomass	Density (no/ha)	Root biomass (t/ha)	Shoot biomass (t/ha)	Roots as % of total biomass
<u>Pinus contorta</u>																
12	Canada	Natural		100		16		17					4, 500	41	133	24
"	"	"		"		25		20	89	6-132	26	15	720	35	195	15
"	"	"		"		6		6	221	0. 1-19	1. 8	19	12, 000	21	92	19
<u>Pinus radiata</u>																
13	Australia	Plantation		9	4-22	13	3-10	8	100	0. 45-24	8. 6	16		11	55	17
14	New Zealand	Plantation		18	19-43	30	20-29	25	8	24-124	56		680	33	271	11
<u>Pinus sylvestris</u>																
5	USSR	-		71		25		24	11					64	216	23
15	Britain	Plantation		7		.5		1	2		.7	45	4, 800	3	4	43
"	"	"		11		4		3	2		2. 5	41	4, 200	11	15	42
"	"	"		14		4		4	2		2. 0	31	5, 200	10	23	30
"	"	"		17		6		5	2		2. 3	26	5, 600	13	35	27
"	"	"		20		7		6	1		2. 6	22	5, 400	14	51	22
"	"	"		23		9		8	1		7. 7	31	3, 600	28	64	30
"	"	"		31		14		13	1		12	22	2, 400	28	100	22
"	"	"		35		15		14	1		23	27	1, 900	44	119	27
"	"	"		55		28		16	1		45	23	760	34	117	23
"	"	Natural		11		1		2	3		.2	21	58, 000	11	41	21
"	"	"		14		3		4	3		.6	31	27, 800	15	34	31
16	Britain	Plantation		33	8-13	10	9-14		17	0. 9-19	7. 3	18		36	150	19
17	USSR	-		100		12		8	10					18	63	22
18	USSR	(Bog)		100		7		5	10					4	33	11

(Continued on next page)

Table 1. (Continued)

Reference	Country	Status	Age		DBH		Height		Sample size	Tree basis: Root biomass			Stand basis			
			Range (yr)	Avg. (yr)	Range (cm)	Avg. (cm)	Range (m)	Avg. (m)		Range (kg)	Avg. (kg)	% of total biomass	Density (no/ha)	Root biomass (t/ha)	Shoot biomass (t/ha)	Roots as % of total biomass
<u>Pseudotsuga menziesii</u>																
19	USA	Plantation		36	2-23			20	18	0.5-34			2,200	32	174	18
20	USA	Natural		30				9					1,200	25	48	34
"	"	"		32				9					1,600	21	36	37
"	"	"		38				14					1,200	10	88	10
"	"	"		38				17					650	17	155	10
"	"	"		52				17					1,200	12	195	6
21	USA	Natural (?)		35	4-18				14	0.1-27						

1. Baskerville 1965
2. Baskerville 1966
3. Honer 1971 a. open-grown b. forest-grown
4. Karizumi 1963
5. Manakov, 1961. 1962a, b <u>in</u> Rodin & Bazilevich 1967
6. Marchenko & Karpov 1961, 1962 <u>in</u> Rodin & Bazilevich 1967
7. Nihlgård 1972
8. Parshevnikova 1957, 1962 <u>in</u> Rodin & Bazilevich 1967
9. Remezov <u>et al</u>. 1959 <u>in</u> Rodin & Bazilevich 1967
10. Rudnova <u>et al</u>. <u>in</u> Rodin & Bazilevich 1967
11. Sonn 1960
12. Johnstone 1971
13. Ovington <u>et al</u>. 1967
14. Will 1966
15. Ovington 1957
16. Ovington & Madgwick 1959
17. Remezov <u>in</u> Rodin & Bazilevich 1967
18. Bazilevich <u>in</u> Rodin & Bazilevich 1967
19. Dice 1970
20. Heilman & Gessel 1963
21. Riekirk 1967

In the few instances where trees older than 100 years were investigated, diameters at breast height (DBH) did not exceed 50 cm. Consequently, extrapolation of the few existing quantitative data to include virgin stands of old-growth northwestern conifers is hardly warranted.

STUDY AREA

The H. J. Andrews Experimental Forest is located approximately 85 km west of Eugene, Oregon in the mid-elevations of the central portion of the western Cascade Mountains. The elevation of the experimental forest extends from 460 to 1640 m in strongly dissected terrain. The average precipitation is approximately 240 cm per year (Rothacher et al. 1967). Rothacher et al. (1967) present a comprehensive description of the climate, geology, and soils typical for the lower elevations. The vegetation at the lower elevations is characterized by communities common to the *Tsuga heterophylla* Zone, while the communities at the higher elevations are predominately those of the *Abies amabilis* Zone, as defined by Franklin and Dyrness (1973). Dyrness et al. (1974) have described in detail the communities of the H. J. Andrews Experimental Forest and neighboring areas within the central western Cascades.

Watershed 10 is a small watershed on the edge of the H. J. Andrews Experimental Forest. The watershed encompasses 10.24 ha, rising in elevation from 420 to 670 m; the drainage flows to the southwest. A more detailed account of the site conditions has been provided by Fredriksen (1972). Watershed 10 contains communities common to the lower elevations of the *Tsuga heterophylla* Zone, and has been described accordingly by Hawk (n. d.). The overstory is dominated by old-growth Douglas-fir. All stems greater than or equal to 15 cm diameter at breast height (DBH) have been stem-mapped for the entire watershed. This stand represents the primary study site of the current modeling efforts of the IBP Coniferous Forest Biome project in Oregon.

METHODS

The approach taken to estimate the total root biomass in a stand containing such large trees was to divide the estimation process into two components: (1) large roots, having a diameter greater than or equal to 10 mm, and (2) small roots, having a diameter less than 10 mm. Large root biomass was estimated from data obtained by directly weighing whole root systems of individual, mature trees. Small root biomass was estimated from soil core samples taken within an old-growth stand. The total root biomass was expressed as the sum of these two components.

Large Root Component

Excavation of the entire root system of an old-growth Douglas-fir is an extremely laborious task. Sampling was restricted to three root systems. To facilitate excavation, accessible and relatively intact root systems of recent windfalls were chosen for this investigation. Each of these systems was carefully excavated using hand tools, hydraulically cleaned, and lifted by crane for weighing. Weight measurements were taken using a dynamometer, or strain gauge, attached between the stump and the crane. The crane's 2270 kg (5000 lb) counter-weight served as a known weight against which to standardize the dynamometer.

Many individual roots were broken during windfall and excavation and remained in the soil. Correction for this loss of biomass was made by tallying the diameters at the point of breakage, and then applying a regression of root weight on root end diameter to the tally of broken root ends on each root system. All broken root ends greater than or equal to 50 mm in diameter were tallied. Broken root ends less than 50 mm were sampled within ten 40 x 40 cm squares, randomly selected from a grid system established on each root system for this purpose. A total of 216 individual, intact roots, ranging in diameter from 2 mm to 190 mm, were cut from the three cleaned systems and were measured for end diameter and fresh weight; any broken root ends present were also noted and appropriate correction was added prior to regression analysis. All diameters, including those for the tally, were measured to the nearest millimeter. Weights were measured to three significant figures. Samples with small fresh weights were weighed to the nearest tenth of a gram.

Finally, each root system was sampled for nutrient and moisture content. Sections of rootstock representing various diameter size classes (in millimeters: < 2, 2-5, 5-10, 10-20, 20-50, 50-100, 100-200, 200-500, and stump) were arbitrarily sampled on each root system. Analysis for nitrogen, phosphorus, potassium, and calcium were performed by the following methods: nitrogen--microkjeldahl (AOAC 1950), phosphorus--molybdenum blue colorimetric method of

Fiske and Subbarow (1925), potassium and calcium--flame emission using a Beckman DU spectrophotometer. The digestion procedure described by Fiske and Subbarow (1925) was used for all analyses. Moisture samples were dried to a constant weight in a 70°C forced-air oven. Moisture content was estimated as the percent of weight lost during oven drying.

Small Root Component

Small roots were estimated on a stand basis in Watershed 10. The sampling procedure, its theoretical basis, and application to forest biomass studies have been described in considerable detail elsewhere (Overton 1973a, b; Overton *et al*. 1973). A brief explanation, however, is contained herein.

Working within the specifications established by IBP, two sample trees were selected from each of the 11 strata defined on the watershed (Brown 1972). An expanding sample of trees was drawn by computer from the stem-map of all stems greater than or equal to 15 cm DBH on Watershed 10. The selection of the sample trees was weighted to represent the larger, dominant overstory trees. The probability of selecting any tree, the "inclusion probability," is proportional to DBH. The inclusion probabilities are dependent upon the number of trees selected, and enable the estimation of a parameter of the stand from the estimate of that parameter in the sampling units. The inclusion probabilities are dependent upon the stratification scheme, but this does not prohibit a post-sampling regrouping of the sample trees, if a different stratification scheme is desired.

The sampling units are defined as the "polygon of occupancy" of the sample trees. The polygon of occupancy is formed by the intersection of the perpendicular lines which pass through the midpoints of the lines connecting the center of the sample tree to the center of the nearest neighboring trees; an example is presented in Figure 1. These polygons define a unique area for each tree. Because no arbitrary distances are used, none of the polygons overlap and no area in the stand is left undefined, no matter how the stocking density of the stand varies.

Small roots were sampled within the polygons of occupancy in the following manner. Samples were taken along the transects to the neighboring trees at locations of 1/2, 1/4, and 1/8 the distance from the center of the sample tree to the center of the neighboring tree. These locations are depicted in Figure 1 by x's. The sample at the midpoint was actually taken immediately within the polygon, not on the boundary. A soil coring device was used to sample small roots. This core sampler takes a soil core 5 cm in diameter and up to 100 cm in length. This sampling device is pictured in Figure 2. Whenever possible, core samples were taken perpendicular to the slope. The depth of each coring was recorded and the core sample was bagged

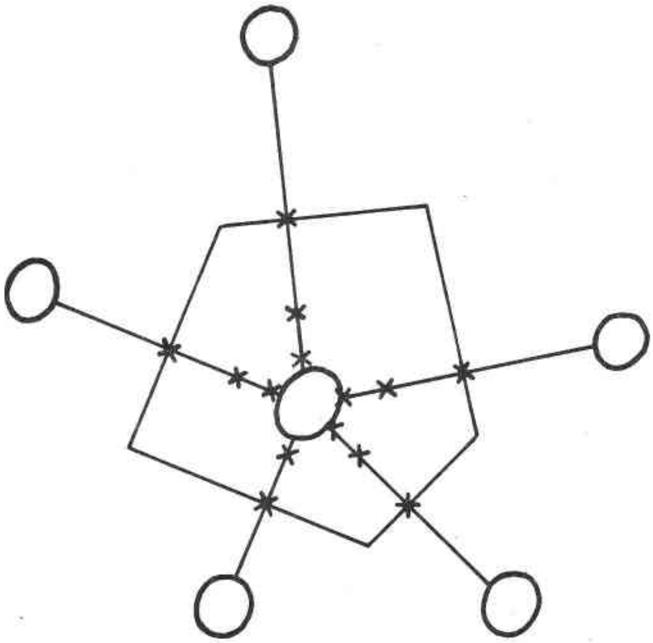


Figure 1. Polygon of occupancy, showing sample points.

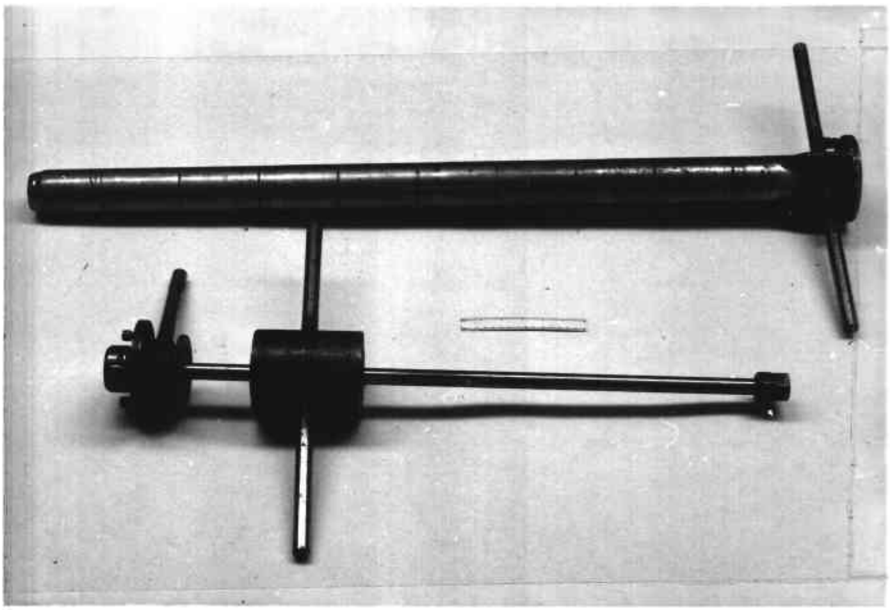


Figure 2. Soil core sampler and slide hammer attachment.

whole, no attempt being made to stratify the soil core. A total of 243 core samples was taken around 22 Douglas-firs in Watershed 10 during late August and early September of 1972.

Few of the soil core samples were sufficiently wet to require drying prior to processing. Each soil core sample was sifted through a set of soil screens (pore sizes in millimeters: 4.00, 1.651, 0.833, and 0.495) to separate the sample into homogeneously sized particle fractions. Each fraction was run through a North Dakota seed blower to separate the roots and organic matter from the heavier soil material. The roots were sorted from the organic matter by hand, using forceps. All identifiable roots were removed from the organic matter. Generally, these included all roots greater than 1 to 2 mm in length and larger than 0.3 mm in diameter. Roots which were obviously decayed were not sorted out; however, beyond this extent, it was not possible to distinguish between roots living at the time of sampling and dead roots. Roots extracted from the soil cores were oven-dried, and then weighed to the nearest milligram in the following diameter size classes: < 5, 5-10, ≥ 10 mm.

Finally, roots extracted from the soil core samples were analyzed for nutrient content. Thirty packets, containing roots extracted from individual core samples, were arbitrarily selected from the packets of roots in the less than 5 mm size class and from the packets of roots in the 5 to 10 mm size class. Analyses for nitrogen, phosphorus, potassium, and calcium were performed as described earlier.

RESULTS

Large Root Component

A description of the three sample trees and the sites on which they were located is presented in Table 2. In all cases, each tree was located close to the edge of a clearcut, and fell as a result of exposure to wind. None of these root systems showed any sign of root rot. Further, there were no other indications to suspect that these individuals were not representative of old-growth and intermediate-aged trees.

Table 3 summarizes the measurements taken and the corrections made during the process of estimating the biomass of the three root systems. The data required to correct for the biomass lost as a result of broken root ends remaining in the soil are presented in Figure 3 and Table 4. Linear regression analysis of the logarithmic transformations of lateral root fresh weight on root end diamter yields the following equation:

$$\text{Log}_{10}\text{Wt (g)} = 2.2260\ \text{Log}_{10}\text{Diam (mm)} - 0.63216 \qquad (1)$$

Correction for broken root ends was made on a fresh weight basis by applying this regression equation to the tally of broken root ends and summing for each root system (see Table 5). One to two meters of

Table 2. Description of the Trees and Sites of the Excavated Root Systems.

Root system number	Age (yr)	DBH (cm)	Height (m)	Site	Elevation	Community type[1/]	Morphology[2/], rooting depth (m)[3/]
1	495	135	67	Road cut adjacent to clearcut margin, steep slope	550	Moist representative of Tshe/Rhma/Gash, indicated by Pomu	Heart root system, 3 m
SOIL[4/]	Frissell loam: Soil is shallow and well drained, consisting of a loam over a gravely loam containing 50% gravels and cobbles in the C horizon (depth to C is 25 cm). Structure is weakly developed, changing from fine granular to subangular blocky to single grain and massive in C. horizon. Parent material is well weathered reddish breccia colluvium. Roots are common in C horizon.						
2	470	110	64	Clearcut margin, gently sloping bench	950	Tshe-Abam/Rhma/Libo	Heart root system, 2 m
SOIL	Carpenter loam: Soil is deep and well drained, consisting of a gravely loam over a stony (50% gravels to boulders) silt loam C horizon (depth to C is approx. 100 cm). Structure is weakly developed, changing from fine granular to subangular blocky to friable massive in C horizon. Parent material is andesitic colluvium.						
3	150	94	58	Seepage area at clearcut margin, gently sloping bench	900	Early successional stage within the Tshe-Abam/Libo habitat type	Flat root system, < 1 m
SOIL	Slipout clay loam: Soil is shallow and poorly drained, consisting of a clay loam over strongly mottled clay B3 and C horizons (depth to B3 is 32 cm; C, 90 cm). Extreme gleying in C, roots rare. Structure is weakly developed, changing from fine granular to subangular blocky to firm massive in B3 and C horizons. Parent material is well weathered greenish breccia.						

1/ As described by Franklin and Dyrness (1973) and Dyrness *et al.* (1974). Species abbreviations: Tshe = *Tsuga heterophylla*, Abam = *Abies amabilis*, Rhma = *Rhododendron macrophyllum*, Gash = *Gautheria shallon*, Libo = *Linnaea borealis*, Pomu = *Polystichum munitum*.

2/ As defined by Köstler *et al.* (1968).

3/ The upper litter level was considered to represent the boundary between the root and trunk. Rooting depth was measured from this point on the excavated root system.

4/ Soil series are provisional (Stephens 1963).

Table 3. Measurements and Corrections Made in Estimating Root System Biomass.

Description	Units	Root system		
		1	2	3
Tree				
Age	yr	495	470	150
DBH	cm	135	110	94
Height	m	67	64	58
Root system				
Lift weight (fresh)	kg	9, 580	5, 510	4, 030
Correction added for broken ends (fresh)	kg	1, 180	832	435
Total fresh weight	kg	10, 760	6, 340	4, 460
Moisture (oven-dry)	%	34. 1	35. 4	38. 9
Total oven-dry weight	kg	7, 090	4, 100	2, 730
Correction subtracted for stump	kg	1, 190	1, 050	340
Oven-dry weight	kg	5, 900	3, 050	2, 390
Fresh weight	kg	8, 950	4, 720	3, 910
Oven-dry weight with 1 m stump	kg	6, 760	3, 580	2, 730

NOTE - The upper litter level was considered to represent the boundary between root and trunk.

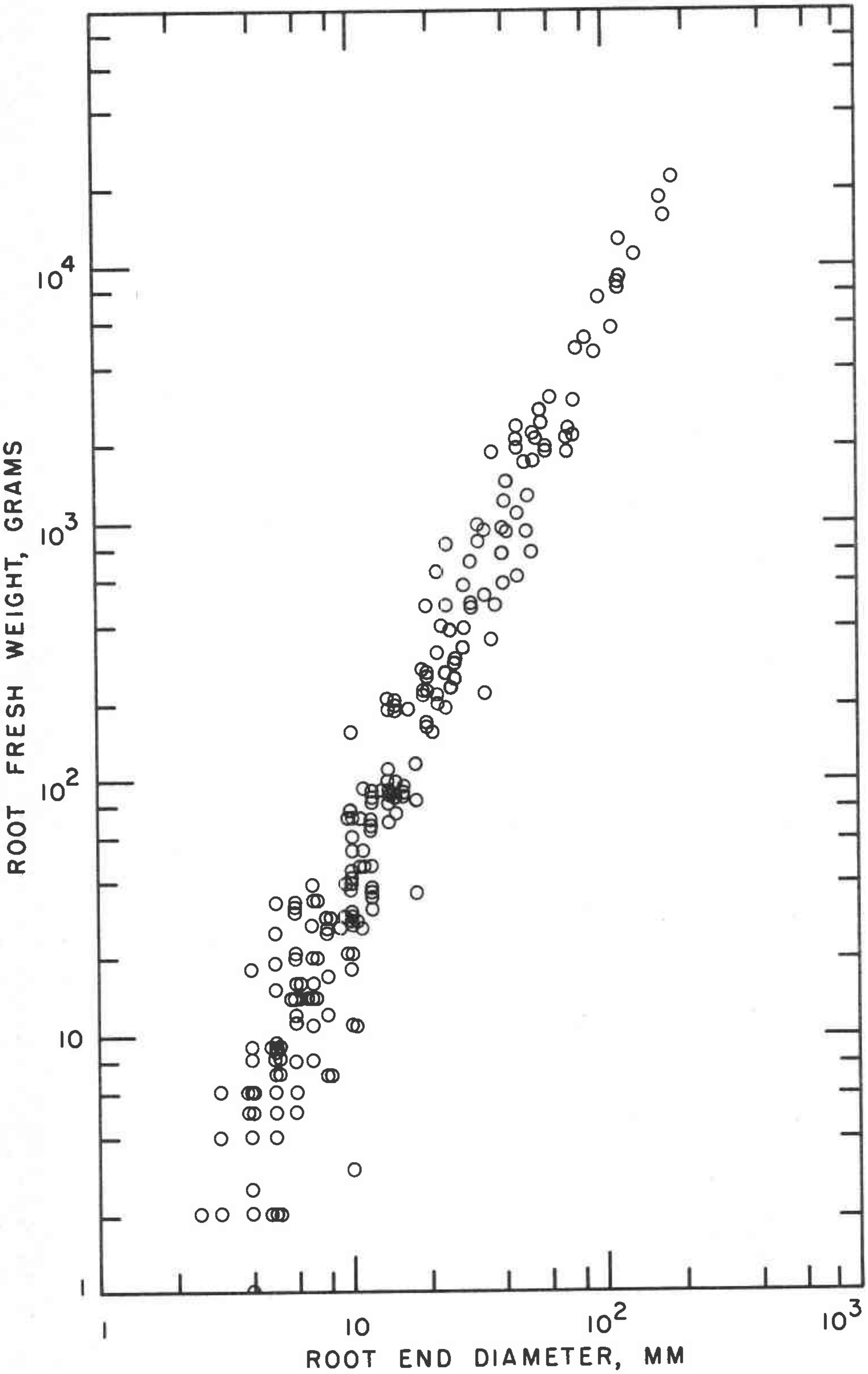


Figure 3. Regression of lateral root fresh weight on root end diameter.

$$Log_{10}Wt\ (g) = 2.2260\ Log_{10}Diam\ (mm) - 0.63216$$

Table 4. Summary of the Tally[1/] of Broken Root Ends.

Root end diameter (mm)	No. of broken root ends		
	Root system		
	1	2	3
<2	19,826	18,094	20,609
2-5	1,373	3,905	3,269
5-10	853	1,615	539
10-20	228	602	231
20-50	63	147	12
50-100	20	32	2
100-200	25	18	5
200-500	11	5	3

[1/] Tally data summed into root end diameter size classes. Number of broken root ends < 50 mm diameter estimated as described in Methods section.

Table 5. Summary of the Correction Added for Broken Ends[1/] Remaining in the Soil.

Root end diameter (mm)	Fresh weight (kg)		
	Root system		
	1	2	3
< 10	59	121	74
10-50	64	145	36
≥50	1,059	566	326
Total	1,182	832	435

[1/] Corrections for individual broken root ends summed into diameter size classes.

stump were left on each root system to facilitate lifting operations. Correction for this stump wood was made by estimating the volume of the remaining trunk, applying the specific gravity of 0.44 (Grier 1973), and subtracting this amount from the total oven-dry weight. The upper litter level was considered to represent the boundary between root and trunk. Because some estimates of aboveground biomass do not include the stump, estimates of the root system biomass with 1 m of trunk are also reported here. On these systems, 1 m added to the upper litter level is approximately equal to the stump at breast height.

Linear regression analysis of the logarithmic transformations of the biomass of the three excavated root systems on stem DBH yields the following equation:

$$\text{Log}_{10}\text{Wt (kg)} = 2.5309\ \text{Log}_{10}\text{DBH (cm)} - 1.6393 \qquad (2)$$

This regression equation was used to estimate the root biomass contributed by a tree having a DBH greater than 50 cm. The root biomass contributed by a tree having a DBH less than or equal to 50 cm was estimated by the "combined Douglas-fir" equation reported by Dice (1970) (converted to kilogram basis):

$$\text{Log}_{10}\text{Wt (kg)} = 2.5786\ \text{Log}_{10}\text{DBH (cm)} - 1.8899 \qquad (3)$$

These regression equations were applied to the frequency distribution of stem DBH to estimate the large root biomass in Watershed 10. The frequency distribution includes the number of stems in 1 cm size classes by species for all stems greater than or equal to 15 cm DBH. These estimates were summed into the following DBH size classes: 15-50, 50-100, and > 100 cm. A summary of the stem data and the subsequent large root biomass estimates is presented in Table 6. Frequency distribution and basal area data were compiled from the stem-map.

Small Root Component

The estimator of small root biomass in Watershed 10 is of the form (Overton et al. 1973)

$$T_y = \sum_S \frac{Y}{\pi} \tag{4}$$

where Y is the biomass of small roots within the polygon of occupancy of the sample tree, π is the inclusion probability of the sample tree, and $\sum_S$ indicates the summation over the sample trees. The small root biomass within the sampled polygon (Y) was estimated as the estimated oven-dry weight of small roots per square meter multiplied by the area of the polygon. The amount of small roots per square meter was estimated from the average oven-dry weight of small roots in the soil core samples taken within the polygon. These data appear in Table 7. Table 8 contains the results of the direct estimation of the small root biomass ($\hat{T}_y$) in the watershed for the area consisting of the polygons of occupancy belonging to Douglas-fir. The total area of the

Table 6. Summary of Stem Distribution Data and Large Root Biomass Estimates for Watershed 10.[1]

Description	Units	DBH size class (cm)			
		15-50	50.1-100	> 100[2]	Total ≥ 15
No. of stems		2,251	242	323	2,816
Proportion		0.799	0.086	0.115	1.000
No. Douglas-fir stems		528	150	315	993
Proportion		0.188	0.053	0.112	0.353
Basal area all stems	m^2	114.1	111.1	411.0	636.2
Proportion		0.179	0.175	0.646	1.000
Basal area Douglas-fir stems	m^2	26.3	80.1	402.8	509.2
Proportion		0.041	0.126	0.633	0.800
Large root biomass, all species[3]	tons	131	331	1,544	2,006
Proportion		0.065	0.165	0.770	1.000
Large root biomass, Douglas-fir	tons	30	245	1,516	1,791
Proportion		0.015	0.122	0.756	0.893
Aboveground biomass, all species DBH ≥ 15 cm (Grier 1973)	tons				6,286
Proportion					1.000
Aboveground biomass, Douglas-fir DBH ≥15 cm (Grier 1973)	tons				5,433
Proportion					0.864

[1] Area of watershed is 10.24 ha.

[2] Maximum DBH = 178 cm

[3] Regression equations (2 and 3, p. 24) for root system biomass of Douglas-fir used for all species.

Table 7. Basic Sample Polygon Data for Estimating Small Root Biomass.

Tree no.	DBH (cm)	Stratum	π	π* [1/]	Polygon area (m^2)	Biomass (kg/m^2) Root diameter 5 mm	5-10 mm
60	29	1	0.0610	0.1084	17.0	0.6746	0.0967
19	57	1	0.1190	0.2115	66.6	0.9898	0.0362
520	126	2	0.0108	0.0182	86.8	1.0316	0.3213
981	86	2	0.0073	0.0123	83.3	1.3004	0.0504
230	148	3	0.0165	0.0270	162.2	0.6151	0.1120
507	104	3	0.0116	0.0190	110.7	0.7704	0.1400
246	120	4	0.0842	0.2254	69.3	0.7546	0.0565
286	146	4	0.1027	0.2749	40.7	0.9420	0.4470
895	141	5	0.0153	0.0276	79.7	0.6619	0.1538
244	77	5	0.0084	0.0152	87.8	0.4710	0.0957
Z55	120	6	0.2172	0.2896	93.7	0.5178	0.0336
202	133	6	0.2392	0.3189	69.4	1.0479	0.1650
378	84	7	0.0287	0.0494	18.6	1.5280	0.1991
891	145	7	0.0493	0.0848	56.8	1.6013	0.3829
331	114	8	0.0271	0.0568	69.6	0.7419	0.1222
7	133	8	0.0316	0.0663	46.3	1.3966	0.2658
98	143	9	0.1337	0.1905	88.9	0.7439	0.0947
912	80	9	0.0743	0.1059	13.8	0.6497	0.0789
1262	92	10	0.0069	0.0116	56.9	1.4297	0.2851
398	150	10	0.0112	0.0189	71.4	1.2108	0.1013
21	89	11	0.0381	0.0628	104.7	1.3946	0.3401
740	137	11	0.0588	0.0970	44.0	1.6889	0.5356

[1/] π* = The inclusion probability for the area defined by the polygons of occupancy belonging to Douglas-fir in Watershed 10.

polygons belonging to Douglas-fir ($\hat{T}_a$) is also estimated by this equation, from which the small root biomass per hectare can be estimated as the ratio

$$\frac{\hat{T}_y}{\hat{T}_a} .$$

This quantity, multiplied by the total measured area of the watershed (or stratum) yields the revised estimate of the small root biomass over all polygons, under the assumption that the average density of small roots within the polygons of occupancy belonging to Douglas-fir and the average density of small roots within the polygons of other tree species are the same. Tables 8 and 9 present the above estimates broken down into 11 strata, as well as the total for the watershed. This stratification is part of the structure of the estimation process. The entire watershed was considered as a single unit. Small root biomass was estimated to be 11.3 t/ha. A negative bias, however, was introduced by the omission of slope correction in the polygon areas used in estimating $\hat{T}_a$.

Large Root Component Estimated from Polygons

The large root biomass from small trees and large shrubs was estimated for the sampled polygons, then expanded as above to represent the entire watershed. A tally of stems, 5 to 15 cm DBH, in the

Table 8. Small Root Biomass and Area Estimates for Polygons Belonging to Douglas-fir in Watershed 10.

Stratum	Area (ha)		Biomass (kg)		
	Total measured	Direct estimate of area occupied by Douglas-fir[1/]	Root diameter		
			< 5 mm	5-10 mm	Total < 10 mm
1	0.188	0.047	418	27	445
2	1.960	1.154	13,727	1,874	15,601
3	2.480	1.183	8,183	1,489	9,672
4	0.242	0.046	372	84	456
5	1.380	0.866	4,632	997	5,629
6	0.096	0.054	396	47	443
7	0.498	0.105	1,648	332	1,980
8	0.660	0.192	1,884	305	2,189
9	0.288	0.060	432	54	486
10	2.120	0.868	11,588	1,781	13,369
11	0.331	0.212	3,091	810	3,901
Total (entire watershed)	10.243	4.787	46,371	7,800	54,171

[1/] Area of polygons belonging to Douglas-fir $(T_a) = \sum_S \frac{A}{\pi^*}$,

π^* = Inclusion probability for area of watershed defined by Douglas-fir.

Table 9. Small Root Biomass Estimate Corrected to Actual Area of Watershed 10.

Stratum	Biomass/hectare (kg/ha) [1]			Total biomass (kg) [2] Root diameter		
	<5 mm	5-10 mm	Total <10 mm	<5 mm	5-10 mm	Total <10 mm
1	8,894	574	9,468	1,672	107	1,779
2	11,895	1,624	13,519	23,315	3,183	26,498
3	6,917	1,259	8,176	17,147	3,119	20,266
4	8,087	1,826	9,913	1,957	443	2,400
5	5,349	1,151	6,500	7,383	1,589	8,972
6	7,333	870	8,203	704	84	788
7	15,695	3,162	18,857	7,817	1,547	9,391
8	9,812	1,589	11,401	6,479	1,048	7,527
9	7,200	900	8,100	2,073	261	2,334
10	13,350	2,052	15,402	28,295	4,349	32,644
11	14,580	3,821	18,401	4,827	1,265	6,092
Total (entire watershed)	9,687	1,629	11,316	99,191	16,685	115,876

[1] From Table 8, estimated biomass divided by estimated area occupied by Douglas-fir.

[2] Biomass per hectare multiplied by total area from Table 8.

sample polygons has been provided by Russel (1973). Equation 3 was applied to this tally to produce the estimates appearing in Table 10. These estimates were expanded in the same manner described for small root biomass (see Tables 11 and 12). Estimates for Douglas-fir, other species, and all species appear in these tables.

Total Root Biomass

The estimate of total root biomass in Watershed 10 is the sum of the large and small root biomass components. The large root biomass was estimated to be 2,006 tons from overstory trees and 25 tons from small trees and large shrubs, for a total large root component of 2,031 tons. Small root biomass was estimated to be 116 tons. These two components sum to 2,147 tons total root biomass, representing an area of 10.24 ha. On a per unit area basis, these estimates equal 198, 11.3, and 210 t/ha for large roots, small roots and total root biomass respectively.

Nutrient Analysis

The results of the nutrient analysis of root samples taken from the excavated systems and from the soil cores are presented in Table 13. These values, representing various diameter size classes, are reported as the percentage of the oven-dry weight. The values for wood and bark, separately, appear for roots 10 mm in diameter and

Table 10. Basic Sample Polygon Data for Estimating Large Root Biomass from Small Trees and Large Shrubs.

Tree No.	Stratum	$\pi*$ [1/]	Biomass (kg)		
			Douglas-fir	Other species	All species
60	1	0.1084	0	1.308	1.308
19	1	0.2115	0	2.353	2.353
520	2	0.0182	5.199	57.439	63.438
981	2	0.0123	0	33.876	33.876
230	3	0.0270	12.301	28.570	40.871
507	3	0.0190	0	20.512	20.512
246	4	0.2254	0	0	0
286	4	0.2749	0	1.045	1.045
895	5	0.0276	0	10.767	10.767
244	5	0.0152	0	8.191	8.191
Z55	6	0.2896	0	2.764	2.764
202	6	0.3189	0	19.027	19.027
378	7	0.0494	0	0	0
891	7	0.0848	17.716	14.312	32.028
331	8	0.0568	0	12.367	12.367
7	8	0.0663	(2.571)[2/]	(13.923)	16.503
98	9	0.1905	15.163	28.788	43.951
912	9	0.1059	0	1.608	1.608
1262	10	0.0116	0	0	0
398	10	0.0189	0	0	0
21	11	0.0628	1.045	35.710	36.755
740	11	0.0970	(2.571)	(13.932)	16.503

[1/] $\pi*$ = Inclusion probability for area defined by polygons belonging to Douglas-fir in Watershed 10.

[2/] Parentheses indicate average values used for the two polygons which were not sampled.

Table 11. Large Root Biomass Estimates for Small Trees and Large Shrubs in Polygons Belonging to Douglas-fir.

Stratum	Area (ha)		Biomass (kg)		
	Total measured	Direct estimate of area occupied by Douglas-fir [1/]	Douglas-fir	Other species	All species
1	0.188	0.047	0	23	23
2	1.960	1.154	286	5,910	6,196
3	2.480	1.183	456	2,138	2,594
4	0.242	0.046	0	4	4
5	1.380	0.866	0	929	929
6	0.096	0.054	0	69	69
7	0.498	0.105	209	169	378
8	0.660	0.192	39	428	467
9	0.288	0.060	80	166	246
10	2.120	0.868	0	0	0
11	0.331	0.212	43	712	755
Total (entire watershed)	10.243	4.787	1,113	10,548	11,661

[1/] Area of polygons belonging to Douglas-fir $(\hat{T}_a) = \sum_{S} \frac{A}{\pi^*}$,

π^* = Inclusion probability for area of watershed defined by Douglas-fir
A = Area of polygon

Table 12. Large Root Biomass Estimates for Small Trees and Large Shrubs Corrected to Actual Area of Watershed 10.

Stratum	Biomass/hectare (kg/ha)[1]			Biomass (kg)[2]		
	Douglas-fir	Other species	All species	Douglas-fir	Other species	All species
1	0	489	489	0	92	92
2	248	5,121	5,369	486	10,038	10,524
3	385	1,807	2,192	955	4,480	5,435
4	0	87	87	0	22	22
5	0	1,073	1,073	0	1,481	1,481
6	0	1,278	1,278	0	123	123
7	1,990	1,610	3,600	379	803	1,182
8	203	2,229	2,432	134	1,471	1,605
9	1,333	2,767	4,100	383	796	1,179
10	0	0	0	0	0	0
11	203	3,358	3,561	67	1,112	1,179
Total (entire watershed)	233	2,203	2,436	2,381	22,563	24,944

1/ From Table 11, estimated biomass divided by estimated area.

2/ Biomass per hectare multipled by total measured area (Table 11).

Table 13. Nutrient Content of Root Samples.

Diameter size class (mm)	Nitrogen (%)	Phosphorus (%)	Potassium (%)	Calcium (%)
Small root component[1/]				
< 5	0.622	0.095	0.173	0.693
5-10	0.262	0.058	0.145	0.547
Large root component[2/]				
< 2	0.443	0.047	0.042	0.384
2-5	0.267	0.029	0.037	0.376
5-10	0.198	0.021	0.032	0.317
10-20	0.135	0.014	0.034	0.196
20-50	0.083	0.007	0.039	0.158
50-100	0.084	0.007	0.032	0.114
100-200	0.064	0.005	0.030	0.111
200-500	0.066	0.005	0.023	0.122
Stump	0.060	0.004	0.022	0.075
Wood only				
10-20	0.109	0.010	0.030	0.116
20-50	0.064	0.004	0.038	0.079
50-100	0.067	0.004	0.031	0.061
100-200	0.049	0.003	0.028	0.047
200-500	0.050	0.003	0.019	0.037
Stump	0.044	0.002	0.018	0.025
Bark only				
10-20	0.240	0.028	0.051	0.517
20-50	0.159	0.018	0.043	0.475
50-100	0.207	0.020	0.038	0.390
100-200	0.145	0.017	0.043	0.445
200-500	0.150	0.017	0.044	0.570
Stump	0.142	0.013	0.041	0.340
Total large root component[3/]	0.084	0.007	0.028	0.130

[1/] Samples from soil cores.

[2/] Samples from excavated systems.

[3/] Rough estimates based on the nutrient data contained in this table and my estimation of the relative proportion of roots in these size classes in Watershed 10.

larger. It was not possible to determine the relative proportions of the total root biomass within the various diameter size classes of roots sampled for nutrient analysis. Thus, the values for the large root component are only rough estimates, based on the nutrient data and my estimation of the relative proportions of roots in these size classes in Watershed 10.

Estimates of the nutrient capital tied up in the roots of a forest are scarce. Aside from the determination of the root biomass of the stand, the greatest obstacle to obtaining such estimates is the difficulty of ascertaining the relative proportions of the root biomass within the various diameter size classes sampled for nutrient analyses. However, considering the paucity of these kinds of data, I have attempted to provide reasonable estimates of nitrogen, phosphorus, potassium, and calcium in the roots of a stand of old-growth Douglas-fir. The nutrient capital tied up in the large root component was estimated by applying the biomass of the large root component to the estimated nutrient values. The nutrient dapital tied up in the small root component was estimated by applying the biomass of the small root component to its measured nutrient values. The results of these calculations and the subsequent estimates of the nutrient content of roots in Watershed 10 are contained in Table 14.

Table 14. Nutrient Capital of Roots in Watershed 10.[1/]

	Root biomass (tons)	Nitrogen (kg)	Phosphorus (kg)	Potassium (kg)	Calcium (kg)
Large root component	2,031	1,710	140	570	2,640
Small root component	116	660	110	190	780
Diameter < 5 mm	99.2	620	100	170	690
Diameter 5-10 mm	16.7	40	10	20	90
Total	2,147	2,370	250	760	3,420
Total per hectare	210	230	24	74	330

[1/] Area of Watershed 10 is 10.24 hectares.

DISCUSSION

Root System Biomass

There are four general approaches to tree biomass estimation: unit area, average tree, stand table, and regression analysis (Ovington et al. 1967, Whittaker and Woodwell 1971). Plantations simplify the problem of estimating total root biomass considerably. Spacing and individual tree dimensions are relatively uniform; each tree may be defined to occupy a nearly regular and constant area of fixed dimensions. Certain assumptions may be reasonably made regarding the species composition, stocking density, and uniformity of the trees in the stand. Average tree techniques (Crow 1971, Ovington 1957) and unit area excavations, or soil block analysis (Karizumi 1968), have been used effectively in these situations. Immature, natural stands also simplify sampling problems though to a lesser degree. Although there is no set spacing, the species composition, stocking density, and individual tree dimensions are relatively uniform. Variation in individual tree dimensions has increased, but is still limited in range. In these situations, the stand table approach provides an improved estimate over the average tree approach (Baskerville 1965). This high degree of homogeneity will often be maintained well into maturity. However, as the stand develops into old-growth, the mortality of mature trees and the establishment of young trees in openings will change the nature of the stand considerably. Species composition, stocking density, and individual tree dimensions often vary widely within old-growth forests. Unit area, average tree, and stand table approaches do not account adequately for the wide variation generally found in old-growth stands. The regression analysis approach most effectively deals with this increased variability and complexity of community structure. Regression analysis is the most widely used approach in all of the above situations. Nearly all comparisons show it to be the most accurate method for estimating plant biomass (Baskerville 1965, Crow 1971, Ovington 1967, Ovington and Madgwick 1959).

Direct measurements of the entire root system of individual, old-growth trees were necessary for this study. Most of the biomass regressions available have been based on small to medium-sized trees, and these regressions cannot be extrapolated with confidence for application to large trees (Whittaker and Woodwell 1971). This is particularly true regarding root biomass. However, the costs of excavating the root systems of standing old-growth Douglas-firs would have been prohibitive. The excavation of suitable, windfall trees was an acceptable alternative. Combined with the study of the lateral root weight versus root end diameter and the tally of broken root ends on each system, this approach permitted a reasonable degree of accuracy without a disproportionate expenditure of time and effort. The tally of broken root ends also serves to describe the condition of the root systems as excavated. The correction represented in the tally is only 11 to 18% of the total oven-dry weight of the root system (see Table 15). The regression equation developed to estimate root system biomass (Eq. 2, p. 24) compares favorably with the "combined Douglas-fir" equation (Eq. 3, p. 24) reported by Dice (1970).

Table 15. Correction for the Total Broken Root Ends as a Proportion of the Root System Biomass.

Description	Root system		
	1	2	3
Oven-dry weight of correction for total broken ends (kg)	779	537	266
Proportion of root system biomass	13%	18%	11%
Proportion of biomass of root system with 1 m stump	11%	15%	10%

Much has been said recently about the use, or misuse, of logarithmic regression equations (Baskerville 1972, Beauchamp and Olson 1973, Halfley 1969, Zar 1968). Baskerville (1972) attributes the source of systematic errors in estimating plant biomass to the discrepancy between arithmetic and logarithmic means. This problem of working with mean values and logarithmic regression equations does not apply to this study. In estimating the large root biomass, the logarithmic regression equation was applied directly to the tally of stems for each of the measured DBH sizes, not to mean values.

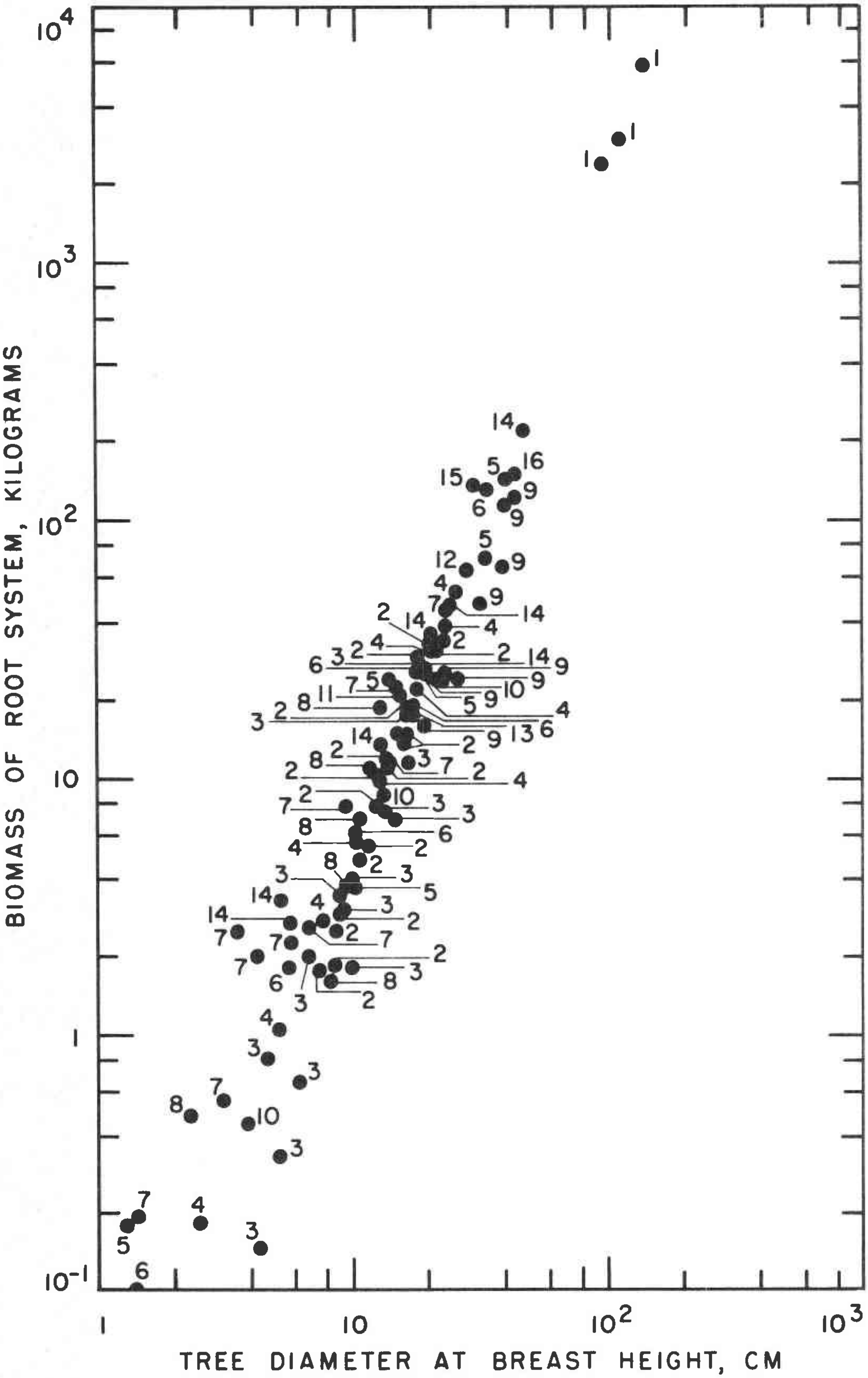
The estimation of large root biomass in Watershed 10 rests mainly on two assumptions: (1) The relationship between DBH and root system biomass is consistent over a wide range of diameter sizes, and (2) the average root biomass of a Douglas-fir and a non-Douglas-fir tree of a given DBH is the same. Being unable to sample over the entire range of DBH and species, these assumptions became necessary. However, they are considered as reasonable in light of the stand structure on Watershed 10 and the exploratory nature of this study. While Douglas-fir makes up only 35% of the number of stems (DBH ≥ 15 cm), these old-growth trees clearly dominate the site in comprising 80% of the basal area, 86% of the aboveground biomass (DBH ≥ 15 cm), and 89% of the large root biomass. Table 6 presents these same comparisons in DBH size classes.

The biomass data from the three root systems excavated for this study are plotted in Figure 4, along with all root system biomass data in the literature available to me. In many papers, the individual root system weights and the corresponding DBH of the trees sampled have not been reported. Rather, the mean value and often the minimum and maximum values only have been published. These values have also been plotted. The key to Figure 4 indicates such references (where mean values have been plotted, the sample size (n) has been listed following the reference). Considering the variety of sources and environmental conditions and the broad range of diameter sizes,

Figure 4. Biomass of root systems.

Key

1	*Pseudotsuga menziesii*	This study
2	" "	Dice 1970
3	" "	Riekirk 1967
4	*Abies balsamea*	Baskerville 1965 (n=89), values from stand table)
5	" "	Honer 1971 Open-grown (n=40, mean, min., & max.) Forest-grown (n=40, mean, min., & max.)
6	*Pinus contorta*	Johnstone 1971 Stands 1 & 2 (n=72, mean, min., & max.) Stand 3 (n=211, mean, min., & max.)
7	*Pinus sylvestris*	Ovington 1957 (n variable, means for different stocking densities)
8	" "	Ovington & Madgwick 1959 (n=17, means for size classes)
9	*Pinus radiata*	Will 1966 (roots ≥ 12.5 mm diam)
10	" "	Ovington *et al.* 1967 (n=100, mean, min., & max.)
11	*Pinus banksiana*	Whittaker & Woodwell 1968 (n=15, mean)
12	*Picea abies*	Nihlgård 1972 (n=3, mean)
13	*Cryptomeria japonica*	Karizumi 1968 (n=10, mean)
14	*Fagus crenata*	Kira & Ogawa 1968
15	*Fagus sylvatica*	Nihlgård 1972 (n-3, mean)
16	*Quercus robur*	Andersson 1972 (n-2, mean)


BIOMASS OF ROOT SYSTEM, KILOGRAMS
TREE DIAMETER AT BREAST HEIGHT, CM
10^4
10^3
10^2
10
1
10^{-1}
1
10
10^2
10^3

these data demonstrate a clear and consistent relationship of root system biomass to stem DBH. Trees with DBH less than 10 cm display considerable variability in root system biomass. However, as the stem DBH increases, this variability decreases, becoming reasonably constant for diameters between 10 and 50 cm. The three root systems excavated for this study provide the only information as to the nature of this relationship for trees with stem diameters at breast height exceeding 50 cm. It is highly unlikely that the nature of the relationship changes dramatically for stem diameters between 50 and 90 cm. Closer examination of the data in Figure 4 suggests that the variation in root system biomass may be as great within a given species as it is between different species of conifers and hardwoods.

Further support for these generalizations appears when regression equations for root system biomass are compared. Regression equations gathered from all sources in the literature available to me are presented in Table 16. Because of the incomplete nature of the published data, the variety of methods used to describe error in arithmetic equivalents for logarithmically transformed data, and the difficulty of evaluating this error, no statistical tests have been applied to compare these equations.

Although some researchers have justifiably expressed concern about the extension of regression relationships far beyond the size

Table 16. Equations for Estimating Root System Biomass from all Available Literature Sources.

Age (yr)	Sample size	B	$Log_{10}A$	r^2	Reference
GENERAL EQUATION:	$Log_{10}Wt\,(kg) = B\,Log_{10}DBH\,(cm) + Log_{10}A$				
Abies balsamea					
42		2.4452	-1.7143		Baskerville 1965 1/
43	89	2.45	0.681	0.92	Baskerville 1966
8-45	40	2.0027	0.0629	0.928	Honer 1971 2/
50-70	40	2.4613	-0.4023	0.898	Honer 1971 3/
Pinus banksiana					
50	40	2.160	-0.2089	0.917	Crow 1971
Pinus rigida					
40	15	2.1325	-3.9119	0.928	Whittaker & Woodwell 1968
Pinus radiata					
18	8	2.4453	-1.9366	0.944	Will 1966*
Pinus sylvestris					
17-55		2.2419	-1.3705	0.968	Ovington 4/*
33	17	2.60	-1.61		Ovington & Madgwick 1959
Pseudotsuga menziesii					
36	18	2.1641	-1.4467	0.908	Dice 1970
	33	2.5786	-1.8899	0.902	Dice 1970 5/
	14	2.9108	-2.3807	0.907	Riekirk 1967*
150 & 480	3	2.5309	-1.6393	0.966	This study
Fagus crenata					
	7	1.9463	-1.9837	0.988	Kira & Ogawa 1968*

(Continued on next page)

Table 16. (Continued)

Age (yr)	Sample size	B	$Log_{10}A$	r^2	Reference
GENERAL EQUATION: $Log_{10}Wt\ (kg) = B\ Log_{10}D^2H\ (cm^2 m) + Log_{10}A$					
Picea abies					
55	3	0.8946	-2.2074	0.990	Nihlgård 1972
Pinus contorta					
100	72	1.022	-1.818	0.949	Johnstone [6/]
100	221	0.806	-1.062	0.900	Johnstone [7/]
Pinus radiata					
18	8	1.0519	-2.9005	0.943	Will 1966*
Pinus sylvestris					
17-55		0.7665	-1.3736	0.966	Ovington 1957 [4/]
Pseudotsuga menziesii					
150 & 480	3	1.0472	-2.6287	0.947	This study
Fagus crenata					
	7	0.6816	-1.0003	0.969	Kira & Ogawa 1968*
Fagus silvatica					
78	3	1.1040	-2.8434	1.000	Nihlgård 1972
Tropical rain forest					
	3	0.775	-1.578		Ogawa et al. 1965

[1/] Linear regression analysis applied to stand table data to derive original equation used to create the stand table, see p. 868 of reference.

[2/] Open-grown

[3/] Forest-grown

[4/] DBH >5 cm

[5/] "Combined Douglas-fir" equation

[6/] Stands 1 and 2 pooled

[7/] Stand 3

*Linear regression analysis applied to these data by me.

range of individuals from which they were developed (Whittaker and Woodwell 1971) or about applying them over broad geographical regions (Honer 1971), the data in Figure 4 and Table 16 suggest that the nature of the relationship of root system biomass to stem diameter at breast height is remarkably consistent. How useful this information is and what levels of accuracy are acceptable will depend upon the objectives of the particular study being planned.

Small Roots Within the Stand

The procedure for sampling small roots in Watershed 10 (Overton 1973a, b; Overton *et al.* 1974) was specifically developed to deal with the problems of sampling in an old-growth stand. This naturally based design has several unique features and advantages. It divides the entire watershed into discrete sampling units, or "polygons of occupancy." This design inherently adjusts to the variations in stocking density within the stand, because the dimensions of the polygon are determined by the proximity of the nearest neighboring trees to the tree in the sampling unit. No arbitrary, fixed distances are used. None of the sampling units overlap, nor is any area left undefined. Of considerable importance to investigators in the field is ease of locating sample points; a distance tape and a diameter tape are the only tools needed. This approach to sampling offers considerable flexibility. Besides biomass studies, it is also appropriate for studies of distribution or dynamics of ecosystem components. The technique permits examination of the spatial distribution of roots around individual trees, as well as the distribution of root biomass between different plant communities within the stand. The productivity, turnover, and seasonal fluctuation in biomass of fine roots can be examined through repeated sampling within the same units. Sampling intensity can be increased by adding additional transects between those to the neighboring trees, as for example, to the corners of the polygons. This sampling procedure is non-destructive. It maintains the integrity of the sampling area and, therefore, does not render these sampling units unsuitable for repeated sampling.

The technique for sampling small roots within the polygons is of a tree-centered design. The nature of the horizontal distribution of small roots was an unknown factor which was accommodated in the sampling plan. A geometric approach to sampling was carried out within the polygons in order to characterize the distribution of small roots as a function of distance from the center of the sample tree and still maintain a uniform density of sampling, regardless of the size of the polygon (Overton 1973b, Overton _et_ _al_. 1974). Linear regression analysis was performed on the small root weights from core samples taken around each of the trees. Little or no correlation was found to exist between the weight of small roots and the distance of the sample point to the center of the sample tree, although roots were not separated according to species. Therefore, the average value of roots per unit area for each of the sampled polygons served as the basis for calculating the small root biomass.

The nature of the soils in the study area was a determining factor in the selection of the means used to extract and process the soil samples containing small roots. The soils on Watershed 10 are well drained, of medium and coarse textures, and have weak structure. In most areas the soils are shallow, only 14% of the core samples taken were 100 cm in depth. Floating stones were not considered to be a problem. The only obstructions to sampling were roots larger than the diameter of the core sampler, though only 9% of the corings encountered this problem. In these instances, the absence of small roots below the obstruction was assumed. The physical properties of these soils permitted the simple and expedient process, described in the Methods section, to separate the roots and organic matter from the soil material. However, most samples contained large quantities of organic material incorporated into the soil. This organic material posed a severe impediment to the separation of small roots, and was overcome only by hand sorting with forceps. This process was extremely time-consuming and tedious, requiring approximately 5 hours per sample. Although flotation techniques have been used successfully (Jenik 1971, Moir and Bachelard 1969, Safford and Bell 1972), these techniques proved to be of little benefit when soil samples contain large quantities of organic material. Undoubtedly, the greatest single time-limiting step in studies of this nature is the processing of soil samples containing small roots.

A comparison of fine root biomass estimates from studies of conifer and hardwood forests is presented in Table 17. Although there is no established convention defining the diameter size of fine roots, nearly all biomass studies are in agreement by defining diameter sizes of fine roots as less than 5 mm. Values generally vary between 5 and 10 t/ha for roots less than 5 mm in diameter when stand age exceeds 10 years. It is somewhat surprising that such a diverse group of sources and environmental conditions would yield data on fine root biomass which are so closely grouped. One might infer that complete occupation of the forest site by fine roots occurs early in stand development, peaks, and levels off as physiological and ecological factors limit fine root biomass per hectare at some upper level, independent of large root and aboveground biomass. To illustrate, not even the estimate of Jenik (1971) for a mature tropical rain forest (total root biomass = 200 t/ha) or that of this study in a 450-year-old stand of Douglas-fir (total root biomass = 210 t/ha, aboveground biomass = 620 t/ha) exceeds the value reported by Ovington (1957) for a 55-year-old plantation of Scots pine (total root biomass = 34 t/ha, aboveground biomass = 117 t/ha). Karizumi (1968) found that the biomass of fine roots peaked then leveled off as stem basal area increased in _Cryptomeria japonica_ plantations.

Table 17. Biomass of Fine Roots.

Country	Age (yr)	Diameter size (mm)	Biomass (t/ha)	Reference
<u>Abies balsamea</u>				
Canada	43	< 2	5.6	Baskerville 1966
<u>Picea abies</u>				
USSR	200	< 1	1.0	Marchenko & Karpov 1962
"	"	1-5	5.4	" " "
"	"	< 5	6.4	" " "
Sweden	55	< 5	2.0	Nihlgård 1972
<u>Picea glauca</u>				
USA	39	≤ 3	7.0	Safford & Bell 1972
<u>Pinus ponderosa</u>				
USA		< 4	4.8	Moir 1965 <u>in</u> Moir & Bachelard 1969
<u>Pinus radiata</u>				
Australia	10	0.4-3	3.4	Moir & Bachelard 1969
"	20	"	3.0	" " "
"	36	"	2.1	" " "
<u>Pinus sylvestris</u>				
Britain	7	< 5	2.9	Ovington 1957
"	11	"	7.6	" "
"	14	"	6.5	" "
"	17	"	5.6	" "
"	20	"	5.2	" "
"	23	"	8.5	" "

(Continued on next page)

Table 17. (Continued)

Country	Age (yr)	Diameter size (mm)	Biomass (t/ha)	Reference
Pinus sylvestris (cont'd)				
Britain	31	< 5	7.9	Ovington 1957
"	35	"	9.6	" "
"	55	"	12.6	" "
"	11	"	7.5	" "
"	14	"	8.6	" "
"	33	"	3.4[1]	Ovington & Madgwick 1959
USSR	32	< 1	3.0	Saurina & Kamenechaja 1969
"		1-5	3.9	" " "
"		< 5	7.0	" " "
Pseudotsuga menziesii				
USA	450	< 5	9.7	This study
Fagus sylvatica				
W. Germany		< 2	2.6	Meyer & Göttsche 1971
" "		2-5	3.9	" " "
" "		< 5	6.4	" " "
Sweden	90	< 5	6.0	Nihlgård 1972
Liriodendron tulipifera				
USA		< 5	≃9	Cox *et al.* 1973
Quercus robur				
Sweden	149	< 5	8.3	Andersson 1971
Tropical rain forest				
Ghana			8-10	Jenik 1971

[1] Sample restricted to top 12.5 cm of soil.

Caution must be exercised when evaluating data on fine root biomass. The results of studies of this nature are generally affected by differences in methodology and the time of year when samples are taken. The isolation of fine roots is a laborious task; shortcuts may create misleading results. The seasonal periodicity of fine root production and turnover results in distinct changes in fine root biomass. Heikurainen (1957) and Kalela (1957), working with Scots pine in Scandinavia, found that fine root biomass decreased by nearly 50% from June to December. While fluctuations were most pronounced in roots with diameters less than 2 mm, these changes also occurred in roots with larger diameters. Changes in roots with diameters less than 2 mm were distinct and rapid in late summer. Larger roots changed to a lesser degree and with no distinct pattern. Heikurainen (1957) observed no changes in roots over 5 mm in diameter. Ovington et al. (1963), studying root biomass in an oak-wood ecosystem in central Minnesota, found essentially the same pattern. Root biomass increased from 12.9 to 20.7 t/ha in the period from April 15 to July 10 and then decreased to 10 t/ha by December. The degree of seasonal fluctiation in fine root biomass varies for different species. Seasonal changes in biomass of roots less than 2 mm in diameter were considerably higher for European beech than for Norway spruce (Göttsche 1972). Finally, the stand age also has an effect on the seasonal change in the amount of fine roots. While Kalela (1957) did not feel he had enough data to conclude that such a trend is characteristic for middle-aged stands of Scots pine, his data are substantial. Studies by Karizumi (1968) further support the idea of stand age affecting the amount of seasonal fluctuation. Unfortunately, interpretation of the data contained in Table 17 is confounded by inadequate information regarding the time of sampling.

Total Root Biomass

Total root biomass in a stand of old-growth Douglas-fir was estimated at 210 t/ha. Referring to Table 1 it is apparent that this estimate greatly exceeds those of previous investigations in coniferous forests. With the exception of Jenik's (1971) studies of mature tropical rain forests in Ghana, previous investigations of root biomass have been restricted to root systems less than 200 kg dry weight with stem diameters at breast height less than 50 cm (see Figure 4). With few exceptions, these data represent immature and boreal forests less than 130 years old. The results of this investigation are not directly comparable to those contained in Table 1 because of the large difference in the size of trees sampled in this study. However, the proportion of root biomass to total plant biomass on a per hectare basis is similar. Roots in Watershed 10 were estimated to comprise 25% of the total plant biomass. This same proportion averaged for the studies compiled in Table 1 equals 23%. The present investigation appears to be the first study of root biomass in old-growth conifers. As such, it provides valuable insight into the nature of root biomass relationships.

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