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# Root biomass studies in forest ecosystems

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With 3 figures

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## 1. 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, and necessary to understand the dynamics of these systems (ANDERSSON 1971). However, biomass determinations are only static, descriptive studies, estimating how much living material is contained in a given space or system at a particular time. Dynamic studies deal with the system, as it functions and generally consist of a series of static studies performed over an interval of time. Dynamic aspects such as growth, productivity, turnover, and so on, may be characterized by monitoring the changes in biomass during these intervals. In this manner, biomass studies may be employed to describe quantitatively the static distribution of materials in ecological systems, and they may also be repeated in sequences to study the dynamic relations of components within 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 of, and has led to attempts for, a better understanding of roots as a part of the entire system. Progress in understanding the belowground portions of ecosystems has lagged, however.

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 of 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. Because of these limitations, most investigations of roots are still exploratory in nature. The approach presented in this paper provides a flexible structure for performing studies of the distribution and dynamics of the belowground components of ecosystems.

The present investigation was carried out as a part of an integrated study by the U. S. International Biological Program. The Coniferous Forest Biome seeks 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 describe quantitatively the total root biomass contained within the rooting zone layer of an old-growth stand of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (MIRB.) FRANCO]. Another objective was 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

Table 1a. Root biomass of coniferous forests

| Reference | Country | Age (yr) | DBH | | Height (m) | Sample size | Root-system biomass | | | Density | Stand biomass | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Range (cm) | Avg (cm) | | | Range (kg) | Avg (kg) | % of total biomass | (no/ha) | Root (t/ha) | Shoot (t/ha) |
| *Abies balsamea* | | | | | | | | | | | | |
| 1 | Canada | 42 | 2—25 | | 2—15 | 89 | 0.2— 53 | | 21—24 | | | |
| 2 | Canada | 43 | | 8 | 8 | 18 | | | | 12,300 | 46 | 154 |
| 2 | Canada | 43 | | 10 | 10 | 19 | | | | 7,400 | 41 | 142 |
| 2 | Canada | 43 | | 11 | 10 | 19 | | | | 4,900 | 38 | 129 |
| 2 | Canada | 43 | | 11 | 9 | 12 | | | | 3,600 | 36 | 113 |
| 2 | Canada | 43 | | 12 | 10 | 13 | | | | 2,800 | 30 | 103 |
| 2 | Canada | 43 | | 14 | 11 | 18 | | | | 1,700 | 30 | 107 |
| 3 a | Canada | 8—45 | 1—40 | 14 | 2—19 | 40 | 0.2—142 | 24 | 20 | | | |
| 3 b | Canada | 50—70 | 10—33 | 19 | 12—23 | 40 | 3.8—72 | 26 | 17 | | | |
| *Cryptomeria japonica* | | | | | | | | | | | | |
| 4 | Japan | 24 | | 17 | 13 | 10 | | 17 | | 1,750 | | |
| *Picea abies* | | | | | | | | | | | | |
| 25 | Belgium | 39 | 25—29 | | 19—20 | 2 | | 51 | 21 | | 38 | 164 |
| 5 | USSR | 24 | | | | | | | | | 20 | 81 |
| 5 | USSR | 38 | | | | | | | | | 38 | 123 |
| 5 | USSR | 60 | | | | | | | | | 65 | 207 |
| 5 | USSR | 93 | | | | | | | | | 65 | 260 |
| 6 | Sweden | 55 | 15—38 | 28 | 18—28 | 3 | | 65 | 15 | 880 | 59 | 308 |
| 7 | USSR | 45—55 | | 19 | | | | | | | 33 | 198 |
| 7 | USSR | 72 | | 18 | | | | | | | 65 | 226 |
| 7 | USSR | 83 | | 26 | | | | | | | 78 | 280 |
| 8 | USSR | 110 | | 17 | 18 | 10 | | | | | 66 | 131 |
| 8 | USSR | 130 | | 20 | 19 | 20 | | | | | 77 | 197 |
| 9 | USSR | 120 | | 15 | 11 | 10 | | | | | 11 | 40 |
| 10 | USSR | 125 | | 24 | 15 | 11 | | | | | 41 | 133 |
| 11 | USSR | 200 | | 35—40 | 30—32 | 20 | | | | | 85 | 225 |
| *Picea rubens* | | | | | | | | | | | | |
| 12 | USA | 87 | | 14 | 9 | 15 | | 31 | 26 | | | |
| *Pinus contorta* | | | | | | | | | | | | |
| 13 | Canada | 100 | 10—33 | 18 | | 72 | 6—132 | 26 | 15 | 4,500 | 41 | 133 |
| 13 | Canada | 100 | | | | | | | | 720 | 35 | 195 |
| 13 | Canada | 100 | 2—17 | 6 | | 221 | 0.1—19 | 1.8 | 19 | 12,000 | 12 | 92 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pinus radiata* | | | | | | | | | | | | |
| 14 | Australia | 9 | 4—22 | 13 | 3—10 | 100 | 0.4—24 | 8.6 | 16 | | 11 | 55 |
| 15 | New Zealand | 18 | 19—43 | 30 | 20—29 | 8 | 24—124 | 56 | | 680 | 33 | 271 |
| *Pinus sylvestris* | | | | | | | | | | | | |
| 16 | Britain | 7 | | 0.5 | 1 | 2 | | 0.7 | 45 | 4,810 | 3 | 4 |
| 16 | Britain | 11 | | 4 | 3 | 2 | | 2.5 | 41 | 4,230 | 11 | 15 |
| 16 | Britain | 14 | | 4 | 4 | 2 | | 2.0 | 31 | 5,190 | 10 | 23 |
| 16 | Britain | 17 | | 6 | 5 | 2 | | 2.3 | 26 | 5,640 | 13 | 35 |
| 16 | Britain | 20 | | 7 | 6 | 1 | | 2.6 | 22 | 5,400 | 14 | 51 |
| 16 | Britain | 23 | | 9 | 8 | 1 | | 7.7 | 31 | 3,640 | 28 | 64 |
| 16 | Britain | 31 | | 14 | 13 | 1 | | 12 | 22 | 2,370 | 28 | 100 |
| 16 | Britain | 35 | | 15 | 14 | 1 | | 23 | 27 | 1,890 | 44 | 119 |
| 16 | Britain | 55 | | 23 | 16 | 1 | | 45 | 23 | 760 | 34 | 117 |
| 16 | Britain | 11 | | 1 | 2 | 3 | | 0.2 | 21 | 58,000 | 11 | 41 |
| 16 | Britain | 14 | | 3 | 4 | 3 | | 0.6 | 31 | 27,800 | 15 | 34 |
| 17 | USSR | 32 | | | | | | | | 4,430 | 26 | |
| 18 | Britain | 33 | 8—13 | 10 | 9—14 | 17 | 0.9—19 | 7.3 | 18 | | 36 | 140 |
| 19 | USSR | 71 | | 25 | 24 | 11 | | | | | 64 | 216 |
| 9 | USSR | 100 | | 12 | 8 | 10 | | | | | 18 | 63 |
| 20 | USSR (bog) | 100 | | 7 | 5 | 10 | | | | | 4 | 33 |
| *Pinus taeda* | | | | | | | | | | | | |
| 21 | USA | 15 | 11—21 | 16 | 10—15 | 7 | | | 16 | | 22 | 90 |
| *Pseudotsuga menziesii* | | | | | | | | | | | | |
| 22 | USA | 35 | 4—18 | 10 | | 14 | 0.1—27 | 6.2 | | | | |
| 23 | USA | 36 | 2—23 | | 20 | 18 | 0.5—34 | | | | | |
| 24 | USA | 30 | | | 9 | | | | | 2,200 | 32 | 174 |
| 24 | USA | 32 | | | 9 | | | | | 1,200 | 25 | 48 |
| 24 | USA | 38 | | | 14 | | | | | 1,600 | 21 | 36 |
| 24 | USA | 38 | | | 17 | | | | | 1,200 | 10 | 88 |
| 24 | USA | 52 | | | 17 | | | | | 650 | 17 | 155 |
| | | | | | | | | | | 1,200 | 12 | 195 |

Table 1a. Root Biomass of Coniferous Forests

Key to references:

1. Baskerville 1965
2. Baskerville 1966
3. Honer 1971, a. open-grown b. forest-grown
4. Karizumi 1968
5. Sonn 1960
6. NihlgÅrd 1972
7. Remezov et al. 1959 in Rodin and Basilevich 1967
8. Parshevnikova 1957, 1961 in Rodin and Basilevich 1967
9. Manakov 1961, 1962a, b in Rodin and Basilevich 1967
10. Rudnova et al. (n. d.) in Rodin and Basilevich 1967
11. Marchenko and Karpov 1961 in Rodin and Basilevich 1967
12. Whittaker et al. 1974
13. Johnstone 1971, stands 1 and 2 pooled for root system data
14. Ovington et al. 1967
15. Will 1966
16. Ovington 1957
17. Saurina and Kameneckaja 1969
18. Ovington and Madgwick 1959a
19. Remezov et al. (n. d.) in Rodin and Basilevich 1967
20. Basilevich (n. d.) in Rodin and Basilevich 1967
21. Ralston 1973, Harris et al. (in press)
22. Riekirk 1967
23. Dice 1970
24. Heilman and Gessel 1963
25. Devillez et al. 1973a

Table 1b. Root Biomass of Deciduous Forests

Key to references:

1. Whittaker et al. 1974
   Mixed eastern deciduous:
   a. Low elevation (550—630 m), *Fagus* — *Acer*
   b. Mid elevation (630—710 m), *Acer* — *Betula* — *Fagus*
   c. High elevation (710—785 m), *Acer* — *Betula* — *Fagus*
2. Zavitkovski and Stevens 1972
3. Basilevich (n. d.) in Rodin and Basilevich 1967
   a. *B. pubescens* with *Populus tremula* (kolok)
4. Ovington and Madgwick 1959b
5. Smirnova and Gorodentseva 1958 in Ovington 1962, Rodin and Basilevich 1967
6. Dzens-Litoskaya 1960 in Rodin and Basilevich 1967
7. Möller et al. 1954
8. NihlgÅrd 1972
9. Ebermeyer 1876, Wetzel 1957, Duvigneaud 1962 in Rodin and Basilevich 1967
10. Garelkov 1973
11. Harris et al. (in press)
12. Miller (n. d.) in Ovington 1962, Miller 1963
13. Remezov et al. 1959 in Rodin and Basilevich 1967, high oak forest (dubrava)
14. Duvigneaud et al. 1971, oak woodland
15. Mina 1955 in Rodin and Basilevich 1967, high oak forest (dubrava)
16. Andersson 1970, oak woodland
17. Ovington et al. 1963, oakwood
18. Sonn 1960
19. Harris et al. 1973, mixed eastern deciduous forests of pine, oak-hickory, chestnut-oak, and yellow poplar
20. Whittaker and Woodwell 1969
21. Devillez et al. 1973b

Table 1b. Root biomass of deciduous forests

| Reference | Country | Age (yr) | DBH Range (cm) | DBH Avg (cm) | Height (m) | Sample size (no.) | Root system biomass Range (kg) | Root system biomass Avg (kg) | Root system biomass % of total biomass | Density (no./ha) | Stand biomass Root (t/ha) | Stand biomass Shoot (t/ha) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acer saccharum* | | | | | | | | | | | | |
| 1 | USA | 79 | | 26 | 18 | 14 | | 121 | 14 | | | |
| *Acer spicatum* | | | | | | | | | | | | |
| 1 | USA | 24 | | 5 | 6 | 15 | | 2.5 | 24 | | | |
| *Alnus rubra* | | | | | | | | | | | | |
| 2 | USA | 33 | | | | | | | | | 52 | 240 |
| *Betula lutea* | | | | | | | | | | | | |
| 1 | USA | 66 | | 25 | 16 | 14 | | 128 | 17 | | | |
| *Betula pubescens* | | | | | | | | | | | | |
| 3a | USSR | 20 | | 8 | 8 | 10 | | | | | 30 | 59 |
| *Betula verrucosa* | | | | | | | | | | | | |
| 4 | Britain | 24 | | 6 | 9 | 1 | | 3.4 | 22 | 4,990 | 17 | 62 |
| 4 | Britain | 42 | | 14 | 13 | 1 | | 19 | 29 | 1,340 | 26 | 69 |
| 4 | Britain | 55 | | 19 | 18 | 1 | | 56 | 23 | 880 | 50 | 164 |
| 3 | USSR | 35 | | 14 | 15 | | | | | | 44 | 169 |
| 5 | USSR | 20 | | | 11 | | | | | | 20 | 61 |
| 5 | USSR | 41 | | 16 | 19 | | | | | | 42 | 207 |
| 5 | USSR | 67 | | | 26 | | | | | | 43 | 171 |
| *Carpinus betulus* | | | | | | | | | | | | |
| 6 | USSR | 46 | | 15 | 17 | | | | | | 58 | 223 |
| *Fagus grandifolia* | | | | | | | | | | | | |
| 1 | USA | 106 | | 23 | 16 | 14 | | 105 | 14 | | | |
| *Fagus sylvatica* | | | | | | | | | | | | |
| 7 | Denmark | 46 | | | 18 | | | | | 3,110 | 26 | 134 |
| 7 | Denmark | 85 | | | 26 | | | | | 320 | 46 | 235 |
| 8 | Sweden | 78 | | 30 | 20 | 3 | | 137 | 13 | | | |
| 8 | Sweden | 45—130 | 12—64 | 39 | 11—29 | 3 | | | | 240 | 51 | 324 |

Table 1b (continued)

| Reference | Country | Age (yr) | DBH Range (cm) | DBH Avg (cm) | Height (m) | Sample size (no.) | Root system biomass Range (kg) | Root system biomass Avg (kg) | Root system biomass % of total biomass | Density (no./ha) | Stand biomass Root (t/ha) | Stand biomass Shoot (t/ha) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 9 | Cen. Europe | 120 | | | | | | | | | 95 | 275 |
| 21 | Belgium | 135 | | 54 | 27 | 1 | | 722 | 22 | | | |
| 21 | Belgium | 120 | 19—60 | 38 | 25 | 1 | | | | 199 | 62 | 269 |
| *Fagus* | | | | | | | | | | | | |
| 10 | Bulgaria | 100 | | 14 | 14 | | | | | 2,500 | 55 | 197 |
| 10 | Bulgaria | 100 | | 18 | 17 | | | | | 2,000 | 38 | 314 |
| 10 | Bulgaria | 100 | | 24 | 24 | | | | | 1,200 | 50 | 441 |
| *Liriodendron tulpifera* | | | | | | | | | | | | |
| 11 | USA | | | | | | | | | | 36 | 130 |
| *Nothofagus truncata* | | | | | | | | | | | | |
| 12 | New Zealand | 110 | | 28 | 21 | 1 | | 77 | | 490 | 39 | 270 |
| *Populus tremula* | | | | | | | | | | | | |
| 13 | USSR | 25 | | 11 | 17 | 11 | | | | | 36 | 150 |
| 13 | USSR | 50 | | 25 | 28 | 11 | | | | | 47 | 258 |
| *Quercus petreae* | | | | | | | | | | | | |
| 14 | Belgium | 117 | | | 24 | | | | | 160 | 55 | 261 |
| *Quercus robur* | | | | | | | | | | | | |
| 6 | USSR | 40 | | 16 | 11 | 11 | | | | | 32 | 123 |
| 15 | USSR | 43 | | 18 | 18 | 10 | | | | | 46 | 109 |
| 13 | USSR | 48 | | 23 | 23 | 10 | | | | | 70 | 191 |
| 14 | Belgium | 35—75 | | | 13—20 | | | | | 1,490 | 35 | 120 |
| 14 | Belgium | 120 | | | 24 | | | | | 110 | 52 | 332 |
| 16 | Sweden | 149 | | 44 | 20 | 3 | | 165 | 16 | | | |
| 16 | Sweden | 125—190 | 32—72 | 50 | 13—39 | 3 | | | | 4,700 | 39 | 201 |
| 15 | USSR | 220 | | 74 | 30 | 10 | | | | | 97 | 406 |
| *Quercus robur* and *Q. petrae* | | | | | | | | | | | | |
| 14 | Belgium | 90 | | | 20 | | | | | 190 | 32 | 154 |
| 14 | Belgium | 90 | | | 21 | | | | | 180 | 35 | 169 |
| 14 | Belgium | 135 | | | 22 | | | | | 420 | 39 | 204 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Quercus rubra* var. *borealis* | | | | | | | | | | |
| 17 | USA | 45—58 | 20 | 17 | | | | | 16 | 165 |
| *Quercus* | | | | | | | | | | |
| 18 | USSR | 22 | | | | | | | 29 | 62 |
| 18 | USSR | 42 | | | | | | | 29 | 141 |
| 18 | USSR | 56 | | | | | | | 38 | 194 |
| 18 | USSR | 200 | | | | | | | 43 | 407 |
| *Tilia cordata* | | | | | | | | | | |
| 16 | Sweden | 42 | 14 | 12 | 3 | 28 | 14 | | | |
| 13 | USSR | 40 | 17 | 18 | 11 | | | | 39 | 120 |
| 13 | USSR | 74 | 28 | 23 | 11 | | | | 55 | 170 |
| Mixed eastern deciduous | | | | | | | | | | |
| 1a | USA | 88 | 24 | 18 | 21 | 120 | 14 | | 31 | 161 |
| 1b | USA | 79 | 25 | 16 | 21 | 116 | 17 | | 32 | 151 |
| 1c | USA | 90 | 23 | 12 | 21 | 83 | 17 | | 24 | 101 |
| 19 | USA | | | | | | | | 33 | 121—137 |
| Oak-pine | | | | | | | | | | |
| 20 | USA | 45 | < 30 | < 16 | | | | 1,850 | 36 | 66 |

Table 1c. Root biomass of tropical and subtropical forests

| | Reference | Country | DBH (cm) | Height (m) | Density: Stem DBH size (cm) | Density (no./ha) | Biomass: Root (t/ha) | Biomass: Shoot (t/ha) |
|---|---|---|---|---|---|---|---|---|
| Tropical rain forest | 1 | Thailand | | < 36 | | | 33 | 371 |
| Tropical rain forest | 1 | Thailand | | < 36 | | | 31 | 295 |
| Tropical rain forest | 2 | Ivory Coast | | | > 3 | 1,840 | 48 | 243 |
| Tropical rain forest | 3 | Ghana | < 310 | < 60 | > 7.6 | 5,300 | 54 | 233 |
| Tropical rain forest | 4 | Ghana | | | | | ≃ 200 | |
| Tropical rain forest | 5 | (Average) | | | | | 101 | 416 |
| Mountain evergreen tropical forest | 6 | Brazil (ev. 1100 m) | | | | 750 | 201 | 860 |
| Mountain evergreen tropical forest | 6 | Brazil (ev. 1500 m) | | | | 900 | 328 | 1,397 |
| Evergreen seasonal forest | 7 | Brazil | < 53 | < 38 | (h > 1.5 m) | 10,100 | 255 | 731 |
| Evergreen seasonal forest | 8 | Cambodia | < 133 | < 45 | > 4.5 | 1,500 | 70 | 345 |
| Evergreen seasonal forest | 8 | Cambodia | < 110 | < 45 | > 4.5 | 1,100 | 51 | 297 |
| Evergreen gallery forest | 9 | Thailand | < 20 | < 29 | | 16,200 | 87 | 291 |
| Temperate evergreen forest | 9 | Thailand | | < 25 | | 2,930 | 53 | 178 |
| Monsoon forest (seasonal evergreen) | 1 | Thailand | | < 36 | | | 25 | 268 |
| Monsoon — savanna forest ecotone | 1 | Thailand | | < 29 | | | 16 | 144 |
| Dipterocarp savanna forest | 1 | Thailand | | < 19 | | | 10 | 69 |
| Dipterocarp savanna forest | 9 | Thailand | | < 25 | | 1,600 | 16 | 51 |
| Mixed savanna forest | 9 | Thailand | | < 25 | | 1,340 | 18 | 59 |
| Savanna | 10 | Ghana | | < 15 | | | 4 | 63 |
| Dry savanna forest | 11 | India | | | | | 11 | 16 |
| Subtropical laurel forest | 12 | Japan | < 25 | 25 | | | 78 | 324 |
| Subtropical deciduous | 5 | (Average) | | | | | 82 | 326 |
| Heath forest (dwarf evergreen) | 8 | Cambodia | < 32 | < 20 | | 2,500 | 19 | 153 |
| *Melaleuca* swamp forest | 8 | Cambodia | < 23 | 10 | | 200 | 4 | 14 |
| *Rhizophora mangel* (mangrove forest) | 13 | Puerto Rico | < 12 | | | | 50 | 63 |
| *Musanga cecropioides* (umbrella tree) | 14 | Congo | | | | | 31 | 121 |

Table 1c. Root Biomass of Tropical and Subtropical Forests

Key to references:

1. OGAWA et al. 1965
2. MÜLLER and NIELSEN 1965 in HOZUMI et al. 1969
3. GREENLAND and KOWAL 1960
4. JENIK 1971
5. RODIN and BASILEVICH 1967
6. RODIN and PRAVDIN (n. d.) in RODIN and BASILEVICH 1967
7. FITTKAU and KLINGE 1973, KLINGE and RODRIGUES 1973
8. HOZUMI et al. 1969
9. OGAWA et al. 1961
10. NYE 1959b in RODIN and BASILEVICH 1967
11. RODIN et al. (n. d.) in RODIN and BASILEVICH 1967
12. KIMURA MAKOTO 1960 in RODIN and BASILEVICH 1967
13. GOLLEY et al. 1962, supporting root above ground considered to be part of shoot
14. BARTHOLOMEW et al. 1953, secondary forest fallow, 18 yrs old

watershed. 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. The results of the analyses of the distribution of root biomass around individual trees and between different plant communities will be presented in a forthcoming paper.

## 2. 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), KOVALEVA (1972), 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 few studies in this latest phase of root investigations have been summarized by OVINGTON (1962) and HERMANN (in press), and in papers presented at symposia sponsored by the USSR ACADEMY OF SCIENCES (1968) and UNESCO (1971).

Systematic investigations of root biomass were begun only during the last two decades. The results of many such investigations pertaining to forest trees have been reported, or referred to, in IUFRO publications on forest biomass studies (YOUNG 1971, 1973). Studies have been conducted in coniferous forests (Table 1a), deciduous forests (Table 1b) of the temperate zone, and tropical and subtropical forests (Table 1c). Published data indicate that root-biomass studies have been conducted mostly on trees less than 100 years old. In the few instances where trees older than 100 years were investigated, diameters at breast height (dbh) did not exceed 54 cm. Consequently, extrapolation of the few existing quantitative data to include virgin stands of old-growth northwestern conifers was hardly warranted.

## 3. Study Area

The H. J. Andrews Experimental Forest is about 85 km west of Eugene, Oregon, in the central portion of the western Cascade Mountains. The elevation of the experimental forest extends from 460 to 1,640 m in strongly dissected terrain. The average precipitation is about 240 cm per year (ROTHACHER et al. 1967). ROTHACHER et al. (1967) have presented 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, and 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 consists of 10.24 ha, rising in elevation from 420 to 670 m; drainage is 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. The overstory is dominated by old-growth Douglas-fir. All stems greater than or equal to 15 cm 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.

## 4. Methods

### 4.0. General remarks

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: large roots, having a diameter greater than or equal to 10 mm; and 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 cores taken within an old-growth stand. The total root biomass was expressed as the sum of these two components. All values reported in this paper are in metric units.

### 4.1. Large-root component

Excavation of the entire root system of old-growth Douglas-firs was therefore restricted to three root systems, ~~Two of which were outside Watershed 10~~. Because destructive sampling was not permitted within Watershed 10, the root systems that were excavated were located elsewhere within the H. J. Andrews Experimental Forest. To facilitate excavation, accessible and mostly intact root systems of recent windfalls were chosen for this investigation. Each of these systems was carefully excavated with hand tools, hydraulically cleaned, and lifted by crane for weighing. Weight measurements were taken by a dynamometer, or strain gauge, attached between the stump and the crane. The crane's 2,270 kg 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. This approach has also been recommended by WHITTAKER and WOODWELL (1968, 1971). 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 40×40 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—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 approximate correction was added before 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 — micro-kjeldahl (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 percentage of weight lost during oven drying.

### 4.2. 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 elsewhere (OVERTON et al. 1973). A brief explanation, however, is provided here.

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 the summation of all tree diameters within the stratum. They permit 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 that pass through the midpoints of the lines connecting the center of the sample tree to the center of the nearest neighboring trees (fig. 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 trees. These locations are depicted

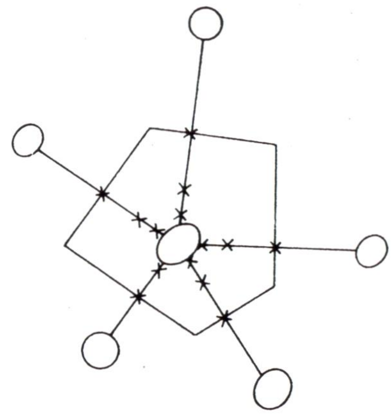

Fig. 1. Polygon of occupancy, showing sample points.

in fig. 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. Whenever possible, core samples were taken perpendicular to the slope. The depth of each coring was recorded, and the core sample was bagged whole with no attempt to stratify the soil core. A total of 243 core samples was obtained 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 before 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 particle fractions of homogeneous size. 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 0.2 mm in diameter. Roots that were obviously decayed were not included, but beyond this, distinguishing between roots living at the time of sampling and dead roots was impossible. Roots extracted from the soil cores were ovendried, and then weighed to the nearest milligram in the following diameter size classes: $< 5$, 5—10, $\geq 10$ 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 243 packets of roots in the less than 5 mm size class and from the 82 packets of roots in the 5 to 10 mm size class. Analyses for nitrogen, phosphorus, potassium, and calcium were performed as described earlier.

## 5. Results

### 5.1. Large-root component

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

Measurements taken and corrections made during the process of estimating the biomass of the three root systems are summarized in table 3. The data required to correct for the biomass lost as a result of broken root ends remaining in the soil are presented in fig. 2 and table 4. Linear regression analysis of the logarithmic transformations of lateral-root fresh weight on root-end diameter 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 (table 5). One to two meters of 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 (personal communication, C. C. Grier, Forest Research Labora-

Table 2. Description of the trees and sites of the excavated root systems

| Root system number | Age (yr) | DBH (cm) | Height (m) | Site | Elevation (m) | 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] | Frisell loam: Soil is shallow and well drained, consisting of a loam over a gravelly loam containing 40% 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 gravelly loam over a stony (40% gravels to boulders) silt loam C horizon (depth to C is about 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 = *Gaultheria 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 (Stepkens, R. R., 1963. Soil and survey report of the H. J. Andrews Experimental Forest. Willamette Nat. For. USDA Fort Ser., Region 6. Unpublished report. 84 p. + map.).

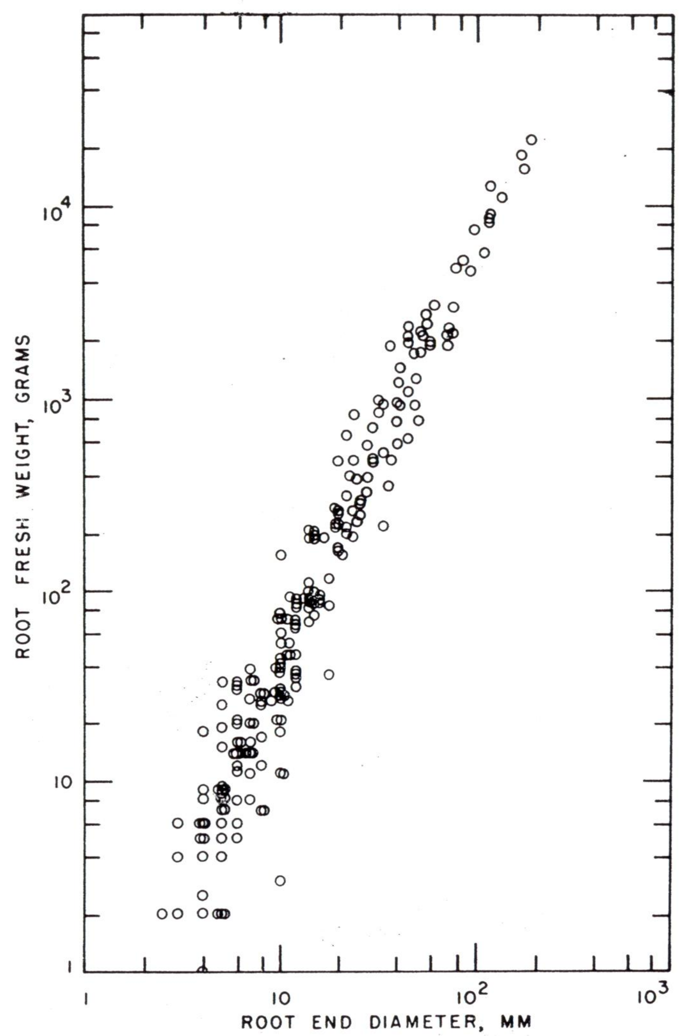


Fig. 2. Regression of lateral root fresh weight on root-end diameter. $\text{Log}_{10}\,\text{Wt}\,(\text{g}) = 2.2260\ \text{Log}_{10}\,\text{Diam.}\,(\text{mm}) - 0.63216$.

tory, Oregon State University), 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 about 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:

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

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) after conversion to kilograms:

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

Table 3. Measurements and corrections made in estimating root system biomass

| Description | Units | Root system 1 | Root system 2 | Root system 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 (ovendry) | % | 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 |
| Equivalent 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.

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 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.

These regression equations were applied to the frequency distribution of stem dbh to estimate the large-root biomass in Watershed 10. The frequency distribution included 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, 51—100, and > 100 cm. A summary of these 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.

Table 6. Summary of stem distribution data and large root biomass estimates for Watershed 10

| Description | Units | DBH size class (cm) | | | |
|---|---|---|---|---|---|
| | | 15—50 | 51—100 | > 100[2] | Total ≥ 15 |
| No. of stems | | 2,251 | 242 | 323 | 2,816 |
| Proportion | | 0.799 | 0.086 | 0.115 | 1.000 |
| No. of 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 | 135 | 344 | 1,519 | 1,998 |
| Proportion | | 0.068 | 0.172 | 0.760 | 1.000 |
| Large root biomass, Douglas-fir | tons | 31 | 256 | 1,479 | 1,766 |
| Proportion | | 0.016 | 0.128 | 0.740 | 0.884 |
| Aboveground biomass, all species DBH ≥ 15 cm[4] | tons | | | | 6,286 |
| Proportion | | | | | 1.000 |
| Aboveground biomass, Douglas-fir DBH ≥ 15 cm[4] | tons | | | | 5,433 |
| Proportion | | | | | 0.964 |

[1] Area of watershed is 10.24 ha.

[2] Maximum DBH = 178 cm.

[3] Regression equations (2, p. 13 and 3, p. 13) for root system biomass of Douglas-fir used for all species.

[4] Personal communication, C. C. Grier, Forest Research Laboratory, OSU.

Table 7. Sample polygon data for estimating small-root biomass

| Tree no. | DBH (cm) | $\pi$[1] | Polygon area ($m^2$) | Biomass ($kg/m^2$), Root diameter < 5 mm | Biomass ($kg/m^2$), Root diameter 5—10 mm |
|---|---|---|---|---|---|
| 60 | 29 | 0.1084 | 17.0 | 0.6746 | 0.0967 |
| 19 | 57 | 0.2115 | 66.6 | 0.9898 | 0.0362 |
| 520 | 126 | 0.0182 | 86.8 | 1.0316 | 0.3213 |
| 981 | 86 | 0.0123 | 83.3 | 1.3004 | 0.0504 |
| 230 | 148 | 0.0270 | 162.2 | 0.6151 | 0.1120 |
| 507 | 104 | 0.0190 | 110.7 | 0.7704 | 0.1400 |
| 246 | 120 | 0.2254 | 69.3 | 0.7546 | 0.0565 |
| 286 | 146 | 0.2749 | 40.7 | 0.9420 | 0.4470 |
| 895 | 141 | 0.0276 | 79.7 | 0.6619 | 0.1538 |
| 244 | 77 | 0.0152 | 87.8 | 0.4710 | 0.0957 |
| 255 | 120 | 0.2896 | 93.7 | 0.5178 | 0.0336 |
| 202 | 133 | 0.3189 | 69.4 | 1.0479 | 0.1650 |
| 378 | 84 | 0.0494 | 18.6 | 1.5280 | 0.1991 |
| 891 | 145 | 0.0848 | 56.8 | 1.6013 | 0.3829 |
| 331 | 114 | 0.0568 | 69.6 | 0.7419 | 0.1222 |
| 7 | 133 | 0.0663 | 46.3 | 1.3966 | 0.2658 |
| 98 | 143 | 0.1905 | 88.9 | 0.7439 | 0.0947 |
| 912 | 80 | 0.1059 | 13.8 | 0.6497 | 0.0789 |
| 1,262 | 92 | 0.0116 | 56.9 | 1.4297 | 0.2851 |
| 398 | 150 | 0.0189 | 71.4 | 1.2108 | 0.1013 |
| 21 | 89 | 0.0628 | 104.7 | 1.3946 | 0.3401 |
| 740 | 137 | 0.0970 | 44.0 | 1.6889 | 0.5356 |

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

### 5.2. Small-root component

The estimator of small root biomass is of the form (OVERTON et al. 1973)

$$\hat{T}_y = \sum_S \frac{Y}{\pi} \tag{4}$$

where Y is the biomass of small roots within the polygon of occupancy of the sample tree, $\pi$ is the inclusion probability of the sample tree, and $\sum_S$ indicates the summation over the sample trees. The small-root biomass within the sampling unit (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. The inclusion probability of an individual tree defining a sampling unit is of the form

$$\pi_i = \frac{x_i \cdot n}{\sum_{N} X} \tag{5}$$

where $x_i$ is the dbh of the tree selected, n is the number of trees selected within the stratum, and $\sum_N X$ is the summation of the dbh of all trees (N) in the stratum. These data (table 7) were applied to Equation 4 to yield the estimates of 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 polygons belonging to Douglas-fir ($\hat{T}_a$) is also estimated by this equation,

$$\hat{T}_a = \sum_S \frac{A}{\pi} \tag{6}$$

where A is the area of the polygon defining the sampling unit. The small-root biomass per hectare can be estimated as the ratio $\hat{T}_y/\hat{T}_a$. This quantity, multiplied by the total measured area of the watershed yields the revised estimate of the small-root biomass over all polygons (table 10), 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. Small-root biomass was estimated to be 99.3, 16.7, and 116 tons for roots $< 5$, 5—10, and $< 10$ mm in diameter. The total area of the polygons belonging to Douglas-fir was estimated as 4.79 ha. A negative bias, however, was introduced by the omission of slope correction in the polygon areas used in estimating $\hat{T}_a$.

### 5.3. Large-root component estimated from polygons

The large-root biomass from small trees and large shrubs was estimated for the sampling units, then expanded as above to represent the entire watershed. A tally of stems, 5—15 cm dbh, in the sample polygons has been provided by RUSSEL (1974). Equation 3 was applied to this tally to produce the estimates of root biomass (table 8). These estimates were expanded in the same manner described for small-root biomass. Estimates of large-root biomass from large shrubs and small trees for Douglas-fir, other species, and all species were 2.4, 22.6, and 25 tons, respectively.

### 5.4. 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 1,998 tons from overstory trees and 25 tons from small trees and large shrubs, for a total large-root component of 2,023 tons. Small-root biomass was estimated to be 116 tons. These two components sum to 2,139 tons total root biomass, representing an area of 10.24 ha. On a unit-area basis, these estimates equal 197.7, 11.3, and 209 t/ha for large roots, small roots, and total root biomass respectively.

Table 8. Estimates of large-root biomass from small trees and large shrubs (DBH = 5—15 cm) in sample polygons

| Tree no. | Biomass (kg)[1] | | |
|---|---|---|---|
| | Douglas-fir | Other species | Total |
| 60 | 0 | 1.308 | 1.308 |
| 19 | 0 | 2.353 | 2.353 |
| 520 | 5.199 | 57.438 | 63.438 |
| 981 | 0 | 33.876 | 33.876 |
| 230 | 12.301 | 28.570 | 40.871 |
| 507 | 0 | 20.512 | 20.512 |
| 246 | 0 | 0 | 0 |
| 286 | 0 | 1.045 | 1.045 |
| 895 | 0 | 10.767 | 10.767 |
| 244 | 0 | 8.191 | 8.191 |
| 255 | 0 | 2.764 | 2.764 |
| 202 | 0 | 19.027 | 19.027 |
| 378 | 0 | 0 | 0 |
| 891 | 17.716 | 14.312 | 32.028 |
| 331 | 0 | 12.367 | 12.367 |
| 7 | (2.571)[2] | (13.923) | (16.503) |
| 98 | 15.163 | 28.788 | 43.951 |
| 912 | 0 | 1.608 | 1.608 |
| 1,262 | 0 | 0 | 0 |
| 398 | 0 | 0 | 0 |
| 21 | 1.045 | 35.710 | 36.755 |
| 740 | (2.571) | (13.932) | (16.503) |

[1] Equals Y in Eq. 4, p. 16.

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

## 5.5. 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 9. 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 larger. Determining the relative proportions of the total root biomass within the various diameter size classes of roots sampled for nutrient analysis was not possible. Thus, the values for the total large-root component are only rough estimates, based on the nutrient data and our subjective estimate of the relative proportions of roots in these size classes in Watershed 10.

Estimates of the nutrient capital contained in the roots of a forest are scarce (Rodin and Basilevich 1967). 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 biomass within the various diameter size classes sampled for nutrient analyses. Considering the paucity of these kinds of data, we have attempted to provide reasonable estimates of nitrogen, phosphorus, potassium, and calcium in the roots of a stand of oldgrowth Douglas-fir. The nutrient capital contained in the large-root component was estimated by applying the biomass of the large-root component to the estimated nutrient values. The nutrient capital contained 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 presented in table 10.

Table 9. 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 | 0.455 |
| 200—500 | 0.150 | 0.017 | 0.044 | 0.570 |
| Stump | 0.142 | 0.013 | 0.041 | 0.340 |
| Total large-root components[3] | 0.084 | 0.007 | 0.028 | 0.130 |

[1] Samples from soil cores.

[2] Samples from excavated systems.

[3] Estimates based on the nutrient data contained in this table and our subjective estimation of the relative proportion of roots in these size classes in Watershed 10.

Table 10. Estimates of the nutrient capital of roots in Watershed 10[1]

| | Root biomass (tons) | Nitrogen (kg) | Phosphorus (kg) | Potassium (kg) | Calcium (kg) |
|---|---|---|---|---|---|
| Large-root component | 2,023 | 1,700 | 140 | 570 | 2,630 |
| 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 | 2,139 | 2,360 | 250 | 760 | 3,410 |
| Total per hectare | 209 | 230 | 24 | 74 | 330 |

[1] Area of Watershed 10 is 10.24 hectares.

## Discussion

### 6.1. Root-system biomass

Biomass of tree components has been estimated through four general approaches: unit-area, average-tree, stand-table, and regression analysis (ART and MARKS 1971, 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, even-aged stands also simplify sampling problems, though to a lesser degree. Although spacing is not set, 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, OVINGTON and MADGWICK 1959a). A high degree of homogeneity will often be maintained well into maturity. As the stand develops into old-growth, however, 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 usually vary widely within old-growth forests and mixed-forest types. Unit-area, average-tree, and stand-table approaches do not account adequately for the wide variation generally found in these situations. The regression analysis approach most effectively deals with this increased variability and complexity of community structure. Regression analysis is the approach most widely used for estimating plant biomass. Nearly all comparisons show it to be the most accurate method (BASKERVILLE 1965, CROW 1971, OVINGTON et al. 1967, OVINGTON and MADGWICK 1959a, MADGWICK 1971).

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 for root biomass. 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 correction for broken roots remaining in the soil, 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. Correction for the loss represented in the tally is equal to 11—18% of the total fresh weight of the root system (computed from table 3). The regression equation developed to estimate root-system biomass (Eq. 2) compares favorably with the "combined Douglas-fir" equation (Eq. 3) reported by DICE (1970).

Logarithmic regression equations are widely accepted and are a requisite for estimations of biomass and production in mixed and uneven-aged stands composed of several species and with a wide range of diameters and heights (ANDERSSON 1970). These equations have been referred to as allometric equations by KIRA and SHIDEI (1967), and the use of them in general is referred to as dimensional analysis by WHITTAKER and WOODWELL (1968, 1971). The objective of their use is to estimate biomass, productivity, or other parameters with suitable accuracy from more easily measured stand or tree dimensions. In investigations where a wide range in the size of individuals exists, the variance associated with successive sizes generally will increase as the dimensions of the individuals increase. This condition violates the assumption of constant variance required for linear regression analysis (BASKERVILLE 1972, DRAPER and SMITH 1966). Logarithmic transformation of the regression variables generally rectifies this problem. However, some controversy has occurred regarding the use 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. In this study, we did not apply logarithmic regression equations to mean values. 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 relies mainly on two assumptions: The relation between dbh and root system biomass is consistent over a wide range of diameter sizes; and the average root biomass of a Douglas-fir and a non-Douglas-fir tree of a given dbh is the same. Because sampling over the entire range of dbh and species was impossible, these assumptions became necessary. They are considered reasonable in light of the stand structure on Watershed 10 and the exploratory nature of this study, however. Although Douglas-firs make up only 35 % of the number of stems (dbh $\geq$ 15 cm), these old-growth trees clearly dominate the site in comprising 80 % of the basal area, 86 % of the above-ground biomass, and 88 % of the large-root biomass (table 6).

The biomass data from the root system excavated for this study have been plotted in fig. 3, along with all root-system biomass data in the literature available to us. These investigations have been restricted to root systems less than 250 kg dry weight from trees with stem diameters less than 55 cm. In many papers, weights of individual root systems 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 been plotted also. Maximum and minimum tree dimensions were assumed to correspond to maximum and minimum biomass values. The key to fig. 3 indicates such references (where mean values have been plotted, the sample size (n) has been listed after the reference). Considering the variety of sources, methods, and environmental conditions, and the broad range of diameter sizes, these data demonstrate a clear and consistent relation of root-system biomass to stem dbh. Trees with dbh less than 10 cm display considerable variability in root-system biomass. As the stem dbh increases, however, this variability decreases, becoming

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Fig. 3. Relation between biomass of root systems and tree diameter at breast height.

Key:

1. *Pseudotsuga menziesii* This study
2. *Pseudotsuga menziesii* DICE 1970
3. *Pseudotsuga menziesii* RIEKIRK 1967
4. *Abies balsamea* BASKERVILLE 1965 (n = 89, values from stand table)
5. *Abies balsamea* HONER 1971, Open-grown (n = 40, mean, min. and max.)
6. *Pinus contorta* JOHNSTONE 1971, Stands 1 and 2 (n = 72, mean min. and max.) Stand 3 (n = 211, mean, min. and max.)
7. *Pinus sylvestris* OVINGTON 1957 (n variable, means for different stocking densities)
8. *Pinus sylvestris* OVINGTON and MADGWICK 1959 (n = 17, means for size classes)
9. *Pinus radiata* WILL 1966 (roots $\geq$ 12.5 mm diam)
10. *Pinus radiata* OVINGTON et al. 1967 (n = 100, mean, min. and max.)
11. *Pinus banksiana* WHITTAKER and 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 and OGAWA 1968
15. *Fagus sylvatica* NIHLGÅRD 1972 (n = 3, mean)
16. *Quercus robur* ANDERSSON 1970 (n = 3, mean)
17. *Acer saccharum* WHITTAKER et al. 1974 (n = 14, mean)
18. *Acer spicatum* WHITTAKER et al. 1974 (n = 15, mean)
19. *Betula lutea* WHITTAKER et al. 1974 (n = 14, mean)
20. *Betula verrucosa* OVINGTON and MADGWICK 1959b
21. *Fagus grandifolia* WHITTAKER et al. 1974 (n = 14, mean)
22. *Nothofagus truncata* MILLER 1963
23. *Picea rubens* WHITTAKER et al. 1974 (n = 15, mean)
24. *Tilia cordata* + *Sorbus acuparia* ANDERSSON 1970 (n = 3, mean)
25. *Fagus sylvatica* DEVILLEZ et al. 1973b

reasonably constant for diameters between 10 and 50 cm. The three root systems excavated for this study provide the only available information as to the nature of this relation for trees with stem dbh exceeding 50 cm. That the nature of this relation would change dramatically for stem diameters between 50 and 90 cm is highly unlikely. Thus, the assumption that the relation is continuous appears reasonable. Closer examination of these data 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 assumptions appears when regression equations for root-system biomass are compared. Regression equations gathered from all sources in the literature available to us are presented in table 11. High correlations are common in logarithmic regressions of dry weight on such tree dimensions as dbh. This is in part because of the balance between apical and radial growth (Bunce 1968), and also because logarithmic units represent progressive orders of magnitude. 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.

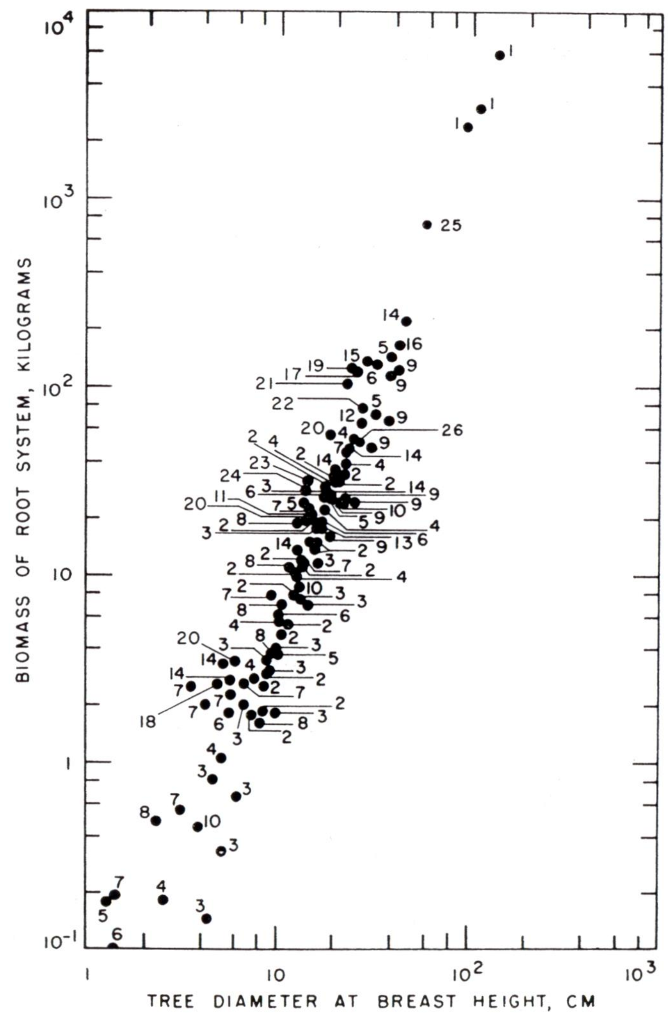

Table 11. Equations for estimating root system biomass from all available literature sources

| 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] |
| *Picea rubens* | | | | | |
| 87 | 15 | 2.1514 | —1.2417 | 0.972 | WHITTAKER et al. 1974 |
| *Pinus banksiana* | | | | | |
| 50 | 40 | 2.160 | —0.2089 | 0.917 | CROW 1971 |
| *Pinus rigida* | | | | | |
| 40 | 15 | 2.1325 | —2.7794 | 0.928 | WHITTAKER and WOODWELL 1968 |
| *Pinus radiata* | | | | | |
| 18 | 8 | 2.4453 | —1.9366 | 0.944 | WILL 1966* |
| *Pinus sylvestris* | | | | | |
| 17—55 | | 2.2419 | —1.3705 | 0.965 | OVINGTON 1957[4]* |
| 33 | 17 | 2.60 | —1.61 | | OVINGTON and MADGWICK 1959 |
| *Pinus taeda* | | | | | |
| 15 | 7 | 3.0742 | —2.6683 | 0.863 | RALSTON 1973 |
| *Pseudotsuga menziesii* | | | | | |
| 36 | 18 | 2.1641 | —1.4467 | 0.908 | DICE 1970 |
| | 33 | 2.5786 | —1.8899 | 0.902 | DICE 1970[5] |
| 35 | 14 | 2.9108 | —2.3807 | 0.907 | RIEKIRK 1967* |
| 150 and 480 | 3 | 2.5309 | —1.6393 | 0.966 | This study |
| *Fagus crenata* | | | | | |
| | 7 | 1.9463 | —1.9837 | 0.988 | KIRA and OGAWA 1968* |
| *Fagus grandifolia* | | | | | |
| 106 | 14 | 2.1478 | —1.1453 | 0.988 | WHITTAKER et al. 1974 |
| *Acer saccharum* | | | | | |
| 79 | 14 | 2.2006 | —1.2632 | 0.992 | WHITTAKER et al. 1974 |
| *Acer spicatum* | | | | | |
| 24 | 15 | 1.7992 | —0.9691 | 0.931 | WHITTAKER et al. 1974 |
| *Betula lutea* | | | | | |
| 66 | 14 | 2.3156 | —1.4000 | 0.981 | WHITTAKER et al. 1974 |
| *Betula verrucosa* | | | | | |
| 24—55 | 3 | 2.3547 | —1.3244 | 0.983 | OVINGTON and MADGWICK 1959b* |
| Seasonal evergreen tropical rain forest | 7 | 2.7766 | —1.8789 | 0.991 | HOZUMI et al. 1965[8]* |
| General Equation: $Log_{10}Wt\,(kg) = B\ Log_{10}D^2H\,(cm^2m) + Log_{10}A$ | | | | | |
| *Picea abies* | | | | | |
| 55 | 3 | 0.8946 | —2.2074 | 0.990 | NIHLGÅRD 1972 |
| *Pinus contorta* | | | | | |
| 100 | 72 | 1.022 | —1.818 | 0.949 | JOHNSTONE 1971[6] |
| 100 | 221 | 0.806 | —1.062 | 0.900 | JOHNSTONE 1971 |
| *Pinus radiata* | | | | | |
| 18 | 8 | 1.0519 | —2.9005 | 0.943 | WILL 1966* |
| *Pinus sylvestris* | | | | | |
| 17—55 | 6 | 0.7665 | —1.3736 | 0.966 | OVINGTON 1957[4] |

Table 11 (continued)

| Age (yr) | Sample size | B | $Log_{10}A$ | $r^2$ | Reference |
|---|---|---|---|---|---|
| General equation: $Log_{10}Wt$ (kg) = B $Log_{10}D^2H$ ($cm^2m$) + $Log_{10}A$ | | | | | |
| *Pseudotsuga menziesii* | | | | | |
| 150 and 480 | 3 | 1.0472 | —2.6287 | 0.947 | This study |
| *Betula verrucosa* | | | | | |
| 24—55 | 3 | 0.9308 | —1.8274 | 0.997 | OVINGTON and MADGWICK 1959 b* |
| *Fagus crenata* | 7 | 0.6816 | —1.0003 | 0.969 | KIRA and 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

[8] Fresh-weight basis

* Linear regression analysis applied to these data by us

Some researchers justifiably have expressed concern about the extension of regression relationships far beyond the size range of individuals from which they were developed (WHITTAKER and WOODWELL 1971) or about applying them over broad geographical regions (HONER 1971). KIRA and SHIDEI (1967) show that different species within a community, and even different species from different localities, may be treated together in the same allometric equation. The data in fig. 3 and table 11 suggest that the nature of the relation 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.

### 6.2. Small roots within the stand

The procedure for sampling small roots in Watershed 10 (OVERTON et al. 1973) was specifically developed to deal with the problems of sampling in an old-growth stand. This sampling 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 the 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

Table 12. Biomass of fine roots

| Country | Age (yr) | Diameter size (mm) | Biomass (t/ha) | Reference |
|---|---|---|---|---|
| *Abies balsamea* | | | | |
| Canada | 43 | < 2 | 5.6 | Baskerville 1966 |
| *Picea abies* | | | | |
| Czechoslovakia | 26 | < 1 | 2.6 | Sika 1969 |
| Czechoslovakia | 26 | 1—10 | 6.8 | Sika 1969 |
| Czechoslovakia | 26 | < 1 | 2.8 | Sika 1969 |
| Czechoslovakia | 26 | 1—10 | 5.7 | Sika 1969 |
| Czechoslovakia | 47 | < 1 | 2.1 | Sika 1969 |
| Czechoslovakia | 47 | 1—10 | 6.3 | Sika 1969 |
| Czechoslovakia | 55 | < 1 | 3.6 | Sika 1969 |
| Czechoslovakia | 55 | 1—10 | 4.6 | Sika 1969 |
| Czechoslovakia | 60 | < 1 | 3.8 | Sika 1969 |
| Czechoslovakia | 60 | 1—10 | 4.9 | Sika 1969 |
| Czechoslovakia | 62 | < 1 | 5.8 | Sika 1969 |
| Czechoslovakia | 62 | 1—10 | 6.5 | Sika 1969 |
| Czechoslovakia | 69 | < 1 | 10.9 | Sika 1969 |
| Czechoslovakia | 69 | 1—10 | 12.2 | Sika 1969 |
| Czechoslovakia | 77 | < 1 | 2.2 | Sika 1969 |
| Czechoslovakia | 77 | 1—10 | 3.6 | Sika 1969 |
| USSR | 200 | < 1 | 1.0 | Marchenko and Karpov 1962 |
| USSR | 200 | 1—5 | 5.4 | Marchenko and Karpov 1962 |
| Sweden | 55 | < 5 | 2.0 | Nihlgård 1972 |
| *Cryptomeria japonica* | | | | |
| Japan | ≃20 | < 2 | ≃1.5 | Karizumi 1968 |
| *Picea glauca* | | | | |
| USA | 39 | ≤ 3 | 7.0 | Stafford and Bell 1972 |
| *Pinus ponderosa* | | | | |
| USA | — | < 4 | 4.8 | Moir 1965 in Moir and Bachelard 1969 |
| *Pinus radiata* | | | | |
| Australia | 10 | 0.4—3 | 3.4 | Moir and Bachelard 1969 |
| Australia | 20 | 0.4—3 | 3.0 | Moir and Bachelard 1969 |
| Australia | 36 | 0.4—3 | 2.1 | Moir and Bachelard 1969 |
| *Pinus sylvestris* | | | | |
| Britain | 7 | < 5 | 2.9 | Ovington 1957 |
| Britain | 11 | < 5 | 7.6 | Ovington 1957 |
| Britain | 14 | < 5 | 6.5 | Ovington 1957 |
| Britain | 17 | < 5 | 5.6 | Ovington 1957 |
| Britain | 20 | < 5 | 5.2 | Ovington 1957 |
| Britain | 23 | < 5 | 8.5 | Ovington 1957 |
| Britain | 31 | < 5 | 7.9 | Ovington 1957 |
| Britain | 35 | < 5 | 9.6 | Ovington 1957 |
| Britain | 55 | < 5 | 12.6 | Ovington 1957 |
| Britain | 11 | < 5 | 7.5 | Ovington 1957 |
| Britain | 14 | < 5 | 8.6 | Ovington 1957 |
| USSR | 32 | < 1 | 3.0 | Saurina and Kamenechaja 1969 |
| USSR | 32 | 1— 5 | 3.9 | Saurina and Kamenechaja 1969 |
| Britain | 33 | < 5 | 3.4[1] | Ovington and Madgwick 1959 a |
| Germany | 65—70 | < 2 | 2.2 | Hausdörfer 1957 |
| Germany | 125 | < 2 | 3.0 | Hausdörfer 1957 |
| Norway | — | < 1 | 1.5[2] | Kohmann 1972 |
| Norway | — | 1—2 | 1.5[3] | Kohmann 1972 |
| *Pinus taeda* | | | | |
| USA | 15 | < 5 | 4.3 | Harris et al. (in press) |

Table 12 (continued)

| Country | Age (yr) | Diameter size (mm) | Biomass (t/ha) | Reference |
|---|---|---|---|---|
| *Pseudotsuga menziesii* | | | | |
| USA | 450 | < 5 | 9.7 | This study |
| USA | 450 | 5—10 | 1.6 | This study |
| *Fagus sylvatica* | | | | |
| W. Germany | — | < 2 | 2.6 | MEYER and GÖTTSCHE 1971 |
| W. Germany | — | 2—5 | 3.9 | MEYER and GÖTTSCHE 1971 |
| Sweden | 90 | < 5 | 6.0 | NIHLGÅRD 1972 |
| *Liriodendron tulipifera* | | | | |
| USA | — | < 5 | ≃ 9 | COX et al. 1973 |
| USA | — | < 5 | 7.6 | HARRIS et al. (in press) |
| *Quercus robur* | | | | |
| Sweden | 149 | < 5 | 6.0 | ANDERSSON 1970 |
| Mixed deciduous | | | | |
| USA | — | < 5 | 7.9 | HARRIS et al. 1973 |
| USA | — | 5—10 | 2.9 | HARRIS et al. 1973 |
| Tropical rain forest | | | | |
| Ghana | — | < 2 or < 5[4] | 8—10 | JENIK 1971 |
| Ghana | — | < 6 | 5.0 | GREENLAND and KOWAL 1960 |

[1] Sample restricted to top 12.5 cm of soil
[2] Sample restricted to top 15 cm of soil
[3] Sample restricted to top 10 cm of soil
[4] Definition of size is unclear

adding additional transects between those to the neighboring trees, as for example, to the corners of the polygons. This sampling procedure is nondestructive. 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 a tree-centered design. The nature of the horizontal distribution of small roots was an unknown factor that was accommodated in the sampling plan. A geometric approach to sampling was carried out within the polygons 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 et al. 1973). 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 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 vertical distributions of roots of forest trees has been examined extensively. The reviews of HERMANN (in press), KOZLOWSKI (1971), LYR and HOFFMAN (1967), and RÖHRIG (1966) indicate that the majority of roots are usually in the upper 50 cm of soil and most of the absorbing roots within the top 20 cm. This information, combined with preliminary observations taken from soil pits, assured us that the 100 cm depth sampling capacity of our soil coring device would be adequate for the needs of this study.

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, overlying a cheese-like, weathering breccia subsoil. 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 appeared to be roots larger than the diameter of the core sampler, though only 9% of the corings were obstructed. 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. Most samples contained large quantities of organic material incorporated into the soil, however. 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 about 6 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 contained 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.

Fine-root biomass estimates from studies of conifer and hardwood forests have been compiled (table 12). Although no established convention defines the diameter size of fine roots, nearly all biomass studies are in agreement by defining fine roots as less than 5 mm in diameter. Values generally vary between 5 and 10 t/ha for roots less than 5 mm in diameter when stand age exceeds 10 years. That such a diverse group of sources, methods, and environmental conditions would yield data on fine-root biomass that are so closely grouped is somewhat surprising. 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 fine-root biomass by 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 = 209 t/ha, aboveground biomass = 620 t/ha) exceeds the value reported by OVINGTON (1957) for a 55-year-old plantation of Scots pine (*Pinus sylvestris*) (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.

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 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 (expressed in terms of root length) decreased by nearly 50% from June to December. Although 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 oakwood 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 November. A different pattern of seasonal periodicity was observed by HARRIS et al. (1973) for a stand of yellow popular (*Liriodendron tulipifera*) in Tennessee. Samples taken over a two-year period showed distinct peaks of 7.5 and 8.3 t/ha during late February and late September, and distinct lows of 2.5 and 4.2 t/ha during late May and December for roots less than 5 mm in diameter. The amount of seasonal fluctuation in fine-root biomass is likely to vary for different species. Seasonal changes in biomass of roots less than 2 mm in diameter were considerably higher for European beech (*Fagus sylvatica*) than for Norway spruce (*Picea abies*) (GÖTTSCHE 1972). Stand age also appears to have an effect on the amount of seasonal change in the biomass of fine roots.

The investigations of KALELA (1957) in Finnish stands of Scots pine showed an increase in seasonal fluctuation to early maturity and a subsequent decrease with advancing age of trees. Studies by KALELA (1950), KARIZUMI (1968), and SIKA (1969) show the amount of fine roots peaking, then declining more gradually as stand age increases. Unfortunately, interpretation of much of the data on the biomass of fine roots is confounded by inadequate information on the time of sampling.

### 6.3. Total root biomass

Total root biomass in an old-growth stand of Douglas-fir was estimated at 209 t/ha. Obviously, this estimate greatly exceeds those of previous investigations of coniferous forests (table 1a). With few exceptions these earlier studies have been restricted to immature and to boreal forests. We were unable to find any data in the literature pertaining to fully mature or old-growth conifer stands. Comparable estimates of root biomass have been reported for mature tropical rain forests in Brazil by RODIN and PRAVDIN (n. d., in RODIN and BASILEVICH 1967), FITTKAU and KLINGE (1973), and KLINGE and RODRIGUES (1973) and also in Ghana by JENIK (1971) (table 1c).

## 7. Conclusions

Previously published data show a remarkably consistent relation between root-system biomass and stem dbh for coniferous and deciduous tree species ranging in diameter from 10 to 50 cm and growing under widely differing environmental conditions. That this relation extends to the huge trees of old-growth forests is perhaps not surprising. Our results support the view of WHITTAKER and WOODWELL (1968) that dimensional analysis is applicable to woodland and forest communities regardless of their composition and size of plants. The ability to estimate root biomass without the need for extraction of entire root systems should greatly enhance future biomass studies in old-growth forests of the Pacific Northwest.

Future ecosystem studies in old-growth stands should be conducted with particular emphasis on the fine-root component. The small proportion of fine-root biomass to total root biomass would indicate that fine-root biomass is stabilized in such stands. We can only speculate as to the reasons for such stabilization. Perhaps it indicates presence of a biological mechanism that controls the balance between the physiologically most active parts of the belowground and aboveground portions of older woody plants. Investigations of productivity, rates of turnover, and of seasonal fluctuations in biomass of fine roots in stands of different ages are needed for confirmation of this hypothesis.

## 8. Summary · Zusammenfassung

A root-biomass study was conducted in an old-growth stand of conifers in the western Cascade Mountains of Oregon. The root systems of three Douglas-firs 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. Biomass of roots less than 10 mm in diameter was estimated from soil cores taken within the stand. The design for sampling small roots was specifically developed to cope with the problems of sampling in old-growth stands. Total root biomass was estimated as 209 t/ha. Nutrient analyses of root samples provided estimates of the nutrient capital contained in the roots of an old-growth stand. The rather consistent relation of root-system biomass to stem diameter at breast height (dbh) for trees between 10 and 50 cm dbh appears also to hold for old-growth Douglas-fir.

**Untersuchungen der Wurzel-Biomasse in Forst-Ökosystemen**

In einem Douglasien-Altholz in den westlichen „Cascade Mountains" von Oregon wurde eine Wurzel-Biomasse-Untersuchung durchgeführt. Das Wurzelsystem von 3 Douglasien mit Durchmessern (in Brusthöhe) von 94, 110 und 135 cm wurde ausgegraben und gewogen, um eine Basis für Regressionsgleichungen zur Schätzung der Wurzeln mit $\varnothing > 10$ mm zu erhalten. Die Biomasse von Wurzeln mit $\varnothing < 10$ mm wurden an Hand des Wurzelgehaltes von Bodenproben, die zwischen den Bäumen entnommen wurden, geschätzt. Der Plan für die Probenentnahme von Feinwurzeln wurde speziell für die Untersuchung von Altholz-Beständen entwickelt. Die totale Wurzel-Biomasse wurde auf 209 t/ha geschätzt.

Nährstoffanalysen der Wurzelproben ergaben Schätzungen des Nährstoffgehaltes in den Wurzeln von Altholz-Beständen. Die ziemlich enge Beziehung zwischen Wurzel-Biomasse und Stammdurchmesser in Brusthöhe (dbh) für Bäume zwischen 10 und 50 cm dbh scheint auch für alte Douglasien zu gelten.

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