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Fine root density distribution and biomass in second- and third-growth Douglas-fir stands on Vancouver Island, British Columbia

Antoine Lalumière and J.A. (Tony) Trofymow

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Contents

List of Figures

List of Tables

Abbreviations

FRB: Fine root biomass per ground area (g/m^2)

FRD: Fine root density (mg/cm^3 soil)

LFH: Surface organic layer

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Abstract

Fine root and ectomycorrhizal root density and biomass were quantified in 2003 and 2004 by sequential soil coring in a 54-year-old second-growth stand and 3- and 14-year-old third-growth stands of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) at Fluxnet–Canada research sites on east–central Vancouver Island, British Columbia. We investigated the relationships of fine root mass and carbon concentration (%C) with soil depth, stand age, and soil substrate. Fine root %C varied significantly with stand age, was lower in the forest floor (LFH) and deeper mineral soil than in shallow soil horizons, and was lower for ectomycorrhizal (EM) versus non-EM roots. These results suggest that differences in root %C associated with soil depth and forest stage should be accounted for when scaling root data for carbon (C) budgets. Total fine root density (mass/soil volume) in the LFH was highest in the 54-year-old stand and declined with depth in mineral soil; whereas total, live, and live conifer root density in the mineral soil was generally highest in the 14-year-old stand, intermediate in the 54-year-old stand, and lowest in the 3-year-old stand. Ectomycorrhizal fine root density was highest in the 54-year-old stand, intermediate in the 14-year-old stand, and lowest in the 3-year-old stand; especially so in the LFH and shallowest mineral soil. Total fine root biomass (mass/area) generally increased with stand age in the LFH, but patterns were less definite in mineral soil. When the LFH and mineral soil were combined, total fine root biomass was lowest in the 3-year-old and highest in the 14- and 54-year-old stands. Ectomycorrhizal fine root biomass was significantly higher in the 54-year-old than in either the 14- or 3-year-old stands. The higher fine root biomass in the 14-year-old stand was unexpected; however, the higher EM root biomass in the 54-year-old stand suggests that a greater proportion of carbon is allocated to the ephemeral absorptive structures of the EM fungi in forests at this age.

Keywords: Fine roots, forest age, soil depth, carbon budgets, ectomycorrhizae, Douglas-fir

Résumé

En 2003 et 2004, on a mesuré la biomasse et la densité des radicelles et des racines ectomycorrhizées en procédant à des séquences de carottage du sol dans un peuplement de seconde venue de 54 ans de Douglas vert (Pseudotsuga menziesii [Mirbel] Franco var. menziesii), aux sites de recherche Fluxnet-Canada situés dans le centre-est de l'île de Vancouver, en Colombie Britannique. On a examiné les relations de la masse des radicelles et de la concentration de carbone (en % de C) avec la profondeur du sol, l'âge du peuplement et le substrat. Le pourcentage de C des radicelles variait de manière significative en fonction de l'âge du peuplement, était plus faible dans le sol forestier (LFH) et dans le sol minéral profond que dans les horizons pédologiques minces, et était plus faible dans les racines ectomycorrhizées (EM) que dans les autres types de racines (« non EM »). Ces résultats laissent supposer que les différences dans les pourcentages de C dans les racines, associées à la profondeur du sol et au stade de développement de la forêt devraient être prises en compte lorsque l'on met à l'échelle les données sur les racines, relatives au bilan de carbone (C). La densité totale des radicelles (masse/volume du sol) dans le LFH était le plus élevée dans le peuplement de 54 ans et diminuait en fonction de la profondeur dans le sol minéral; par ailleurs, la densité totale, la densité d'arbres vivants et la densité des racines de conifères dans le sol minéral étaient généralement le plus élevées dans le peuplement de 14 ans, de valeur moyenne dans le peuplement de 54 ans et le plus faible dans le peuplement de 3 ans. La densité des radicelles ectomycorrhizées était le plus élevée dans le peuplement de 54 ans, de valeur moyenne dans le peuplement de 14 ans et le plus faible dans le peuplement de 3 ans, et c'était notamment le cas dans le LFH et dans le sol minéral le plus mince. En général, la biomasse totale des radicelles (masse/superficie) augmentait avec l'âge du peuplement dans le LFH, mais les profils étaient moins nets dans le sol minéral. Quand le LFH et le sol minéral étaient associés, la biomasse totale des radicelles était le plus faible dans le peuplement de 3 ans et le plus élevée dans les peuplements de 14 et de 54 ans. La biomasse des radicelles ectomycorrhizées était nettement plus élevée dans le peuplement de 54 ans que dans les peuplements de 14 ou de 3 ans. La biomasse plus élevée des radicelles dans le peuplement de 14 ans est un résultat inattendu; cependant, la biomasse plus élevée des racines ectomycorrhizées (EM) dans le peuplement de 54 ans laisse supposer qu'une plus forte proportion de carbone est allouée aux structures absorbantes éphémères des champignons ectomycorrhiziens dans les forêts de cet âge.

Mots clés : radicelles, âge de la forêt, profondeur du sol, bilans de carbone, ectomycorrhize, Douglas vert

1. Introduction

The importance of fine roots to total ecosystem carbon (C) and nutrient cycles in forests is well documented for several tree species and in many geographical areas (Ammer and Wagner 2005; Fogel and Hunt 1979; Klopatek 2002; Santantonio and Hermann 1985; Vogt et al. 1982, 1998, 1996). Fine root turnover is an important source of C to forest soils (Rasse et al. 2001); estimates of fine root and mycorrhizal turnover are as much as three times higher than that of foliage, branches, and boles combined (Fogel and Hunt 1979). Fine root density and biomass typically increase with stand age (Grier et al. 1981; Sylvia and Jarstfer 1997; Vogt et al. 1983a) until canopy closure when they stabilize or decrease slightly (Vogt et al. 1987, 1983a, 1983b). In general, density and biomass of fine roots and mycorrhiza decrease with increasing soil depth (Curt et al. 2001; Grier et al. 1981; Harley 1969; Kurz and Kimmins 1987; Olsthoorn and Tiktak 1991; Persson 1980; Sainju and Good 1993; Santantonio and Hermann 1985; Sylvia and Jarstfer 1997; Vogt et al. 1981), and most mycorrhizal roots occur in the organic litter layer or just below it (Goodman and Trofymow 1998; Jonsson et al. 2000; McMinn 1963; Persson 1980; Vanninen and Mäkelä 1999). Fine root density and biomass decrease with decreasing soil nutrient concentrations (Curt et al. 2001; Sainju and Good 1993), and trees on poor sites generally allocate more of their biomass to fine roots and mycorrhizae than trees on richer sites (Haynes and Gower 1995; Keyes and Grier 1981; Klopatek 2002; Kurz and Kimmins 1987; Vanninen and Mäkelä 1999; Vogt et al. 1983a, 1987). Santantonio and Hermann (1985) found that standing crops of fine roots increased with site moisture for mature Douglas-fir stands in Oregon.

While some studies report that fine root biomass is a small fraction of either total tree biomass or ecosystem carbon budgets, a consensus has not been reached (Janssens et al. 1999; Keyes and Grier 1981; Vogt et al. 1982). An accurate determination of fine root biomass is an important component of such budgets. There is a lack of data on the effects of site conditions and stand developmental stage on fine roots and mycorrhizae and their distribution in the soil (Santantonio and Hermann 1985). Differences in trends for fine root biomass with increasing stand age between mineral soil and forest floor, and between high- and low-productivity stands (Vogt et al. 1983b), suggest further study should investigate the factors responsible for the observed differences and whether the trends apply across other stands.

Measurements of fine root biomass are logistically demanding because they require sufficient soil cores that are carefully washed and processed to obtain reliable data; however, such data are critical for determining total ecosystem live biomass stocks. Single annual samples do not allow for determination of fine root production, which requires repeated sampling and processing within the same year (Persson 1980; Santantonio et al. 1977). Interpretation of these results can also be difficult due to large variation between samples, small sample sizes, potential for loss of small roots, and issues with scaling information taken from cores up to the level of an entire stand (Bengough et al. 2000). Indirect sampling methods, such as the use of minirhizotrons, allow for repeated non-destructive observations of root systems, but can be expensive and must be verified with quantitative measures (Bengough et al. 2000; Hendricks et al. 1993). Thus, while single annual root sampling is insufficient to determine root production, the root density distribution results can be used to allocate fine root production values obtained by other methods to different soil layers, and for interpretation of measurements such as soil respiration. Therefore, even with the limitations of the fine root soil core method as described above, the method does yield estimates of fine root biomass that can be readily compared to values in the majority of other published studies that have used similar methods, and can also be used to determine the fraction of the standing stock live biomass in fine roots.

The objectives of this study were to:

1. Quantify fine root biomass and density distribution from the surface organic layer (LFH) to 55 cm depth in mineral soil for different fine root classes including ectomycorrhizal roots;
2. Test whether the vertical distributions and total mass of the component root classes change with increasing stand age, by comparing clearcut (3-year-old), pole/sapling (14-year-old), and young, mid-rotation (54-year-old) stands;
3. Determine the carbon concentration (%C) of fine roots, and see if it differs between substrates, soil depths, stand ages, and root types, and if so, determine what the implications are;
4. Examine how the thickness of the organic LFH layer varies between stands of different ages to see if that may account for differences in total fine root biomass in the LFH between the stands; and
5. Compare our estimates of root biomass to others from similar temperate forest types.

The results presented here represent an important component in determining total ecosystem C stocks at sites and stations of the Fluxnet–Canada Research Network, where net ecosystem production is estimated using flux towers and measurements of C stocks and stock changes

(Fluxnet–Canada 2003). Data from this study will also be used to expand upon and corroborate future results from other research done at the Fluxnet–Canada coastal BC station including:

- estimating the vertical profile distribution of fine root production from monthly minirhizotron measurements,
- estimating net primary production,
- partitioning of autotrophic and heterotrophic respiration,
- measuring vertical profile distributions of soil respiration and water uptake, and
- testing and creating parameters for models that estimate the annual C budget for flux tower sites at this station.

2. Material and Methods

2.1 Site Description

Field sampling was conducted in 12 established 60 × 60 m permanent sample plots (subsites), four for each structural stage, at the Fluxnet–Canada coastal BC station, located in the Oyster River and Buckley Bay areas of Vancouver Island, British Columbia, Canada (Table 1). These sites are in the driest subzone (CWHxm) of the Coastal Western Hemlock biogeoclimatic zone (CWH), which has a mean annual rainfall of 1500 mm and mean annual temperature of 9.1°C (Pojar et al. 1991).

The large, young, mid-rotation stand (DF1949) located at the Oyster River site covers a range of edaphic site conditions (Table 1) and is characterized by a Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) overstorey with some western redcedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.). The understorey is dominated by salal (*Gaultheria shallon* Pursh), sword fern (*Polystichum munitum* [Kaulf.] K.B. Presl), red huckleberry (*Vaccinium parvifolium* Sm.), and twinflower (*Linnaea borealis* L.). The topography is steeply to strongly sloping. The original old-growth stand was logged and slash was broadcast burned between 1937 and 1943. The site was planted in 1949 and fertilized once in 1994. Dominant trees at this site averaged about 54 years old at the time of sampling.

Two sites, one at the Oyster River area (HDF1990) and one at Buckley Bay (HDF1988), are the locations for the third-growth pole/sapling stands. Collectively, they cover a range of edaphic site conditions (Table 1) and represent an earlier stage of succession than the young, mid-rotation forest. The Oyster River pole/sapling stand was planted with Douglas-fir in 1990 after harvesting the second-growth stand and burning slash piles in 1989. The understorey is dominated by salal, trailing blackberry (*Rubus ursinus* Cham. & Schlecht.), red huckleberry, and vanilla-leaf (*Achlys triphylla* [J.E. Smith] DC.). Slope ranges from 0 to 2%, with moderately to strongly rolling topography. The Buckley Bay pole/sapling stand was planted in 1988 with Douglas-fir, but western redcedar, western hemlock, red alder (*Alnus rubra* Bong.), and bigleaf maple (*Acer macrophyllum* Pursh.) are also present. The understorey is dominated by thimbleberry (*Rubus parviflorus* Nutt.), bracken fern (*Pteridium aquilinum* [L.] Kuhn), and twinflower. The topography is moderately rolling to strongly sloping. The previous second-growth stand on this site was harvested in 1987, and in 1988 slash piles were burned and the site was planted. The site was then fill-planted in 1991 and treated with herbicide in 1992. Trees at these sites averaged about 14 years old at the time of sampling and are collectively referred to as the 14-year-old stands.

The third-growth clearcut stand (HDF2000) located at Oyster River spans three different kinds of edaphic site conditions (Table 1) ranging from a flat, gravely fluvial terrace to more complex topography with undulating to moderately rolling terrain. A permanent plot was installed on each of the edaphic sites. Salal and grasses are present in all stands, which were planted with Douglas-fir in 2000 following harvesting and burning of slash piles in 1999. The previous second-growth stands, cut in 1999, were originally established in 1932 following harvest of the old-growth forest in 1929 and slash burning in 1930. Trees at these sites averaged about 3 years old at the time of sampling.

2.2 Field Sampling Procedure

All field sampling was performed from May 20 to June 3, 2003 and May 4 to 12, 2004. A total of 12 permanent plots were sampled; four in each structural stage (Table 1). Three vertical sequential soil cores were extracted near the soil pit in each of three subplots (each a National Forest Inventory-style sample plot, NFI 2004) per permanent sample plot. Each core was 55 cm deep, divided into five sub-cores: organic LFH layer (D0), shallow mineral layer (D5), and three deeper 15-cm mineral soil layers (D20, D35, and D50). Only complete cores to 50 cm were taken; if a rock was hit, the core was abandoned and another core was taken. Each sub-core was put into a labelled plastic bag. The surface 0–10 cm organic/mineral core was extracted with a 5.0-cm diameter intact soil corer, the thickness of the organic and mineral samples were measured, and then the core was separated into the D0 and D5 sub-cores. The deeper sub-cores were extracted with steel corers (3.5 cm inner diameter). Samples were stored at 2°C until processed.

Table 1. Permanent sample plot locations on east Vancouver Island and their stand and soil characteristics.

Stand Structural Stage	Fluxnet Site ID	Plot – Stand #	Lat. (˚N)	Long. (˚W)	Elev. (m)	Year Est.	Age at 2003 (yr)	Mean Live Tree Sampling (m)	Mean Live Stem Height (#/ha)	Mean Live Basal Density (m^2/ha)	Moisture Regime Area	Nutrient Regime	% Coarse Fragment Volume (> 25mm)*	% Coarse Fragment Volume (> 2mm)	% Sand **	% Silt **
Clearcut (CC)	HDF2000	31	49.897	125.384	175	2000	3	<2	933	n/a	Submesic	Rich	13	34	75	19
	HDF2000	32	49.917	125.380	170	2000	3	<2	2000	n/a	Submesic	Rich	26	46	79	14
	HDF2000	33	49.939	125.358	170	2000	3	<2	1650	n/a	Submesic/ Mesic	Rich	12	25	65	27
	HDF2000	41	49.982	125.447	210	2000	3	<2	1750	n/a	Subxeric/	Rich Submesic	9	28	62	23
Pole/Sapling (PS)	HDF1990	21	49.987	125.344	175	1990	13	3.1	3267	3.8	Submesic	Medium	3	25	83	12
	HDF1990	22	49.990	125.376	175	1990	13	3.3	2900	3.7	Submesic	Medium	0	11	67	22
	HDF1988	61	49.563	124.909	165	1988	15	4.0	1150	2.1	Subxeric/	Rich Submesic	7	13	46	31
	HDF1988	62	49.573	124.931	180	1988	15	4.5	1650	4.4	Xeric/	Rich Subxeric	8	18	50	27
Young Forest (YF)	DF1949	11	49.892	125.366	310	1949	54	28.3	717	50.5	Submesic/	Rich Mesic	2	15	54	22
	DF1949	12	49.896	125.335	290	1949	54	22.9	975	54.8	Mesic	Rich	4	30	66	25
	DF1949	14	50.003	125.398	370	1949	54	17.7	1567	60.4	Mesic	Medium	5	24	57	26
	DF1949	18	49.907	125.474	285	1949	54	18.5	883	51.6	Mesic/	Rich Subhydric	3	11	49	26

* Values by depth were used as the cfp (coarse fragment proportion) for calculating root biomass per square metre. See equation 2.
**Gravimetric basis.

2.3 Laboratory Processing Procedure

All laboratory processing was performed from May 26 to July 28, 2003 and May 28 to September 3, 2004. Each sub-core was washed through a sieve (1.70 mm opening size). All roots were removed and stored cold in distilled water until sampled (within two days). For each sub-core, fine roots (< 2 mm diameter) were spread out in a thin layer of water on a 17 x 26 cm plastic tray with 15 equally spaced ruled lines 17 cm long on the bottom of the tray (total line length was 255 cm). All roots intersecting all lines were classified into one of five categories: 1) dead; 2) conifer ectomycorrhizal, but now dead; 3) conifer ectomycorrhizal live; 4) conifer non-ectomycorrhizal live; or 5) non-conifer live. In most cases 100 or more roots were scored. In cases where there were less than 100 intersections, all roots in the tray were classified. Classification was based on root morphology, colour, turgidity, strength, and the presence of a white vascular strand (Grier et al. 1981; Keyes and Grier 1981; Kurz and Kimmins 1987; Persson 1978; Reynolds 1970). Fine roots from container-grown Douglas-fir, western redcedar, and salal were examined before sampling in 2004 to assist in determining coniferous/non-coniferous status. Failure to have verified this prior to the 2003 sampling may have resulted in erroneously inflated biomass and density values for the live conifer category in 2003. All roots (including mycorrhizae) were decanted from the trays, dried at 70°C for at least 48 hours in an oven, and the total dry mass was measured to 10^{-4} g. For the 2003 samples, roots from each sub-core were ground and a LECO CR12 Total Carbon Analyzer was used to determine %C. A sample of roots from 2004 was also separated by root category and substrate, and roots from each category were dried, ground, and analyzed for %C with a LECO CNS2000 Elemental Analyzer.

2.4 Data Analysis

For each sub-core, fine root density (FRD, mg/cm^3 soil) was calculated as follows:

$$[1]\quad FRD\ (mg/cm^3) = \frac{Root\ mass\ (g)}{\pi r(cm)^2 \cdot thickness\ (cm)} \cdot 1000 mg/g$$

where *r* is the core radius. Because of the varying thickness of the mineral horizon in the D5 sub-core, a nominal thickness of 5 cm was used to calculate fine root biomass (FRB, root biomass per ground area, g/m^2) for that layer. The deeper mineral sub-cores measured 15 cm in thickness. Since the mineral soil cores exclude coarse fragments (> 2.5 cm), a correction factor was applied to account for the coarse fragment proportion (cfp) in each soil layer as determined from previous measurements of the soil pit in each subplot. The calculation was as follows:

$$[2]\quad FRB\ (g/m^2) = \frac{FRD\ (mg/cm^3) \cdot thickness\ (cm) \cdot (1\text{-}cfp) \cdot 10000(cm^2/m^2)}{1000 mg/g}$$

The total biomass of fine roots in the LFH layer, the entire mineral soil to 55 cm, and the LFH layer and mineral soil combined was calculated for each core.

From the five root categories sampled, four fine root classes were defined for subsequent analysis: 1) total (live and dead), 2) live, 3) live conifer, and 4) live conifer ectomycorrhizal (hereafter referred to as ecto). For each sub-core, the proportion of fine roots in each class was calculated and multiplied by total fine root density or biomass to obtain the fine root density or biomass in each root class.

Mean values of LFH thickness, fine root density, and fine root biomass for each plot are available in supplementary tables online (Appendix I, II). All statistical analyses were performed using Statistical Analysis Software (SAS Institute 2002), with α=0.05. Analysis variables were normally distributed or nearly so. Fine root density variances tended to increase slightly with increasing density, and fine root biomass variances tended to increase through the three structural stages and decrease over the two sample years.

A one-way repeated measures ANOVA (analysis of variance) was used to test the null hypothesis that there was no difference in the LFH layer thickness between structural stage and sampling year, because of the potential effect of LFH layer thickness on LFH fine root biomass.

For the 2003 samples, a two-way ANOVA was used to investigate differences in fine root %C between structural stages and soil depths. A one-way ANOVA and a pooled *t*-test were used to investigate differences in fine root %C between root classes and substrates, respectively, for the small root sample from 2004.

Two-way repeated measures ANOVAs investigated the null hypothesis that there was no difference in mean fine root density in the LFH in each root class between structural stage and sampling year. We also examined differences in fine root density distribution with structural stage and sampling year for each root class, while accounting for the effect of mineral soil depth. To do this, we used fine root density means for each subplot to generate least-squares quadratic equations for each soil depth:

Fine Root Density = $\beta_0 + \beta_1$(Soil Depth) + β_2(Soil Depth)^2. For each coefficient estimate, the four plot means per structural stage were used to test the null hypothesis that there was no difference in the mean coefficient estimate with structural stage and sampling year using two-way repeated measures ANOVAs.

Two-way repeated measures ANOVAs investigated the null hypothesis that there was no difference in mean fine root biomass in each root class between structural stage, substrate, and sampling year. Two-way repeated measures ANOVAs investigated the null hypothesis that there was no difference in mean fine root biomass (for all substrates combined) in each root class between structural stages and sampling year.

The Student-Newman-Keuls (SNK) multiple comparison test investigated differences in means between structural stage, substrates, and/or sampling year, where applicable.

3. Results

3.1 LFH Thickness

There was a significant interaction between sampling year and structural stage when partitioning variation in LFH thickness between stages (P=0.0325). Thickness of the LFH was lower in 2004 than in 2003 in the clearcut stand and the young forest stand, but higher in 2004 in the pole/sapling stand (Table 2).

Table 2. Mean thickness of the LFH layer (cm ±1 S.E.) in clearcut, pole/sapling, and young forest Douglas-fir stand structural stages in 2003 and 2004. There was a significant interaction between sampling year and structural stage (P=0.0325).

	Stand Structural Stage		
Year	**Clearcut**	**Pole/Sapling**	**Young Forest**
2003	4.4 (1.3)	3.1 (0.9)	4.6 (1.3)
2004	3.2 (0.4)	4.5 (0.5)	4.2 (0.4)

3.2 Fine Root Carbon Concentration

The main effects of both structural stage and soil depth were significant (both P<0.0001). Fine root %C (all soil depths) was significantly lower in the pole/sapling stand (44.59 ± 0.35%) than in either the clearcut stand (48.44 ± 0.38%) or the young forest stand (47.70 ± 0.31%), which were not significantly different from each other. Fine root %C (all structural stages) was significantly lower in the shallowest mineral horizon (D5) than in the organic LFH layer and the deeper mineral horizons (Table 3).

For the small sample of roots from 2004, there was a significant difference in fine root %C between live non-conifer (50.0 ± 2.0%, n=4), live conifer non-ectomycorrhizal (49.6 ± 1.5%, n=4), and live conifer ectomycorrhizal (47.5 ± 0.9%, n=3) fine roots (P<0.0001). Live conifer ectomycorrhizal roots had a lower %C than both live non-conifer and live conifer non-ectomycorrhizal roots but, due to small sample sizes and the lower power of the SNK test compared to the *F*-test

Table 3. Mean carbon concentration (%C) of total fine roots from five soil depths in clearcut, pole/sapling, and young Douglas-fir stands for 2003 and 2004. Means sharing a letter (A or B) are not significantly different (SNK).

Soil Depth	N	Mean %C (±1 S.E.)
D0 (LFH)	36	47.64 (0.48) A
D5 (mineral)	35	44.92 (0.46) B
D20 (mineral)	35	46.93 (0.48) A
D35 (mineral)	35	47.68 (0.56) A
D50 (mineral)	32	47.09 (0.52) A

(Underwood 2001), the differences were not statistically significant. Carbon concentration was not significantly different between organic (LFH) and mineral substrates (t_g= -1.47, P=0.1748).

3.3 Fine Root Density Distribution

Mean total fine root density (FRD) in the LFH was significantly higher in 2003 than in 2004 (P=0.0377), and ranged from a high of 5.8 mg/cm^3 in 2003 in the young forest stand to a low of 2.2 mg/cm^3 in 2004 in the clearcut stand. In 2004, the clearcut and pole/sapling stands had higher total FRD in the LFH than in the shallow mineral soil (D5). In the mineral soil, mean total FRD declined with increasing depth, with the highest values always in the pole/sapling stand and the lowest always in the clearcut stand, except at the lowest depth (Figure 1a). The intercept term (β_0) of the regression equations for total FRD against mineral soil depth was significantly different between structural stages (Table 4a), indicating significant differences in mean total FRD with structural stage (Figure 1a).

Mean live FRD in the LFH was significantly higher in 2003 than in 2004 (P=0.0016), and ranged from a high of 5.0 mg/cm^3 in 2003 in the young forest stand to a low of 1.5 mg/cm^3 in 2004 in the clearcut stand. In 2004 in the clearcut and pole/sapling stands, live FRD was greater in the shallow mineral soil (D5) than in the LFH. The intercept term of the regression equations for live FRD versus mineral soil depth differed significantly with structural stage and sampling year (Table 4b).

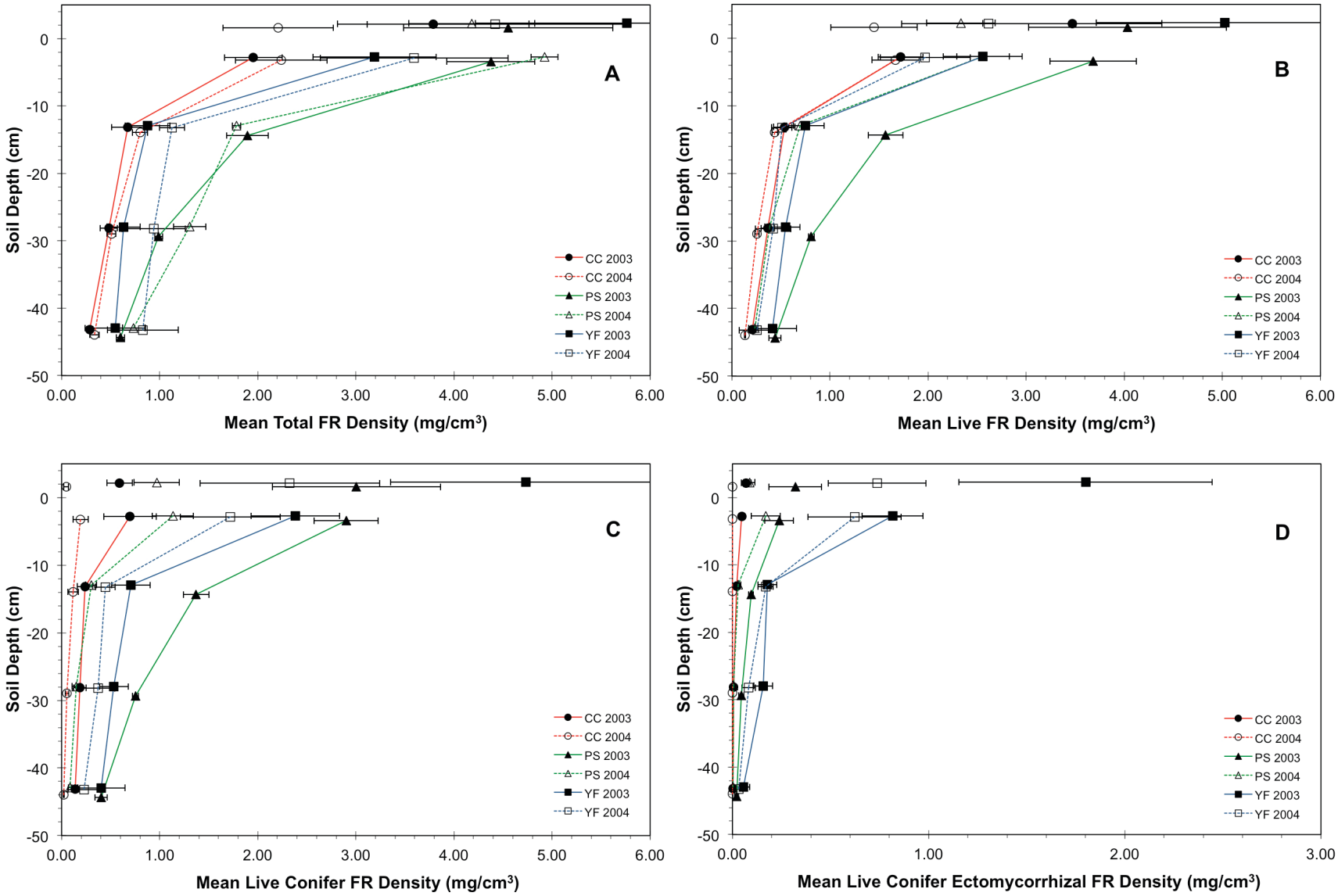

Figure 1. Distribution of mean (± 1 S.E.; n=4 per datum) A) total (live and dead); B) live; C) live conifer; and D) live conifer ectomycorrhizal (LCE) fine root (FR) density (mg/cm3) with soil depth, within clearcut (CC), pole/sapling (PS), and young forest (YF) Douglas-fir stand structural stages on east–central Vancouver Island, BC, Canada in 2003 and 2004. Note reversed y axes on all and scale change in D.

Table 4. Summary of two-way repeated measures ANOVAs on the intercept, linear, and quadratic coefficients of regression equations of the form Fine Root Density = $\beta_0 + \beta_1$(Mineral Soil Depth) + β_2(Mineral Soil Depth)^2 between clearcut, pole/sapling, and young Douglas-fir structural stages and years (2003 and 2004) for total, live, live conifer, and live conifer ectomycorrhizal root classes (n=4 per stage, per year).

		Regression Coefficient					
		β_0		β_1		β_2	
Source	**DF**	*F*	**P**	*F*	**P**	*F*	**P**
a) Total							
Between Subject Effects							
Stage	2	6.68	0.0167*	3.70	0.0671	3.45	0.0771
Error	9						
Within Subject Effects							
Year	1	1.51	0.2502	0.63	0.4480	0.66	0.4364
Year × Stage	2	0.05	0.9519	0.05	0.9499	0.16	0.8506
Error	9						
b) Live							
Between Subject Effects							
Stage	2	5.92	0.0228*	3.28	0.0849	2.46	0.1410
Error	9						
Within Subject Effects							
Year	1	7.51	0.0228*	1.23	0.2958	0.41	0.5378
Year × Stage	2	3.04	0.0980	0.65	0.5459	0.49	0.6274
Error	9						
c) Live Conifer							
Between Subject Effects							
Stage	2	9.46	0.0061	7.40	0.0126*	6.58	0.0174*
Error	9						
Within Subject Effects							
Year	1	35.82	0.0002	16.22	0.0030*	11.37	0.0082*
Year × Stage	2	6.65	0.0168*	0.87	0.4512	0.04	0.9596
Error	9						
d) Live Conifer Ectomycorrhizal							
Between Subject Effects							
Stage	2	11.91	0.0030*	10.21	0.0048*	9.46	0.0061*
Error	9						
Within Subject Effects							
Year	1	2.00	0.1910	0.83	0.3862	0.60	0.4573
Year × Stage	2	0.23	0.8016	0.35	0.7131	0.59	0.5736
Error	9						

Note: *significance at α=0.05 for highest-order term in ANOVA.

Across all depths and stages, mean live FRD was significantly higher in 2003 than in 2004. Across years and depths, live FRD was highest in the pole/sapling stand and lowest in the clearcut stand (Figure 1b).

Mean live conifer FRD in the LFH was significantly higher in 2003 than in 2004 across all stages (P=0.0014), was significantly higher in the young forest stand than in the clearcut stand over both years (P=0.0311), and ranged from 0.1 mg/cm3 in 2004 in the clearcut stand to 4.7 mg/cm3 in 2003 in the young forest stand. Live conifer FRD was greater in shallow mineral soil (D5) than in the LFH in 2004 in the clearcut and pole/sapling stands, and in 2003 in the clearcut stand only. In the mineral soil, FRD decreased with depth for all stages, and was highest in the pole/sapling stand in 2003 (Figure 1c). A significant interaction was observed between sampling year and structural stage for the intercept term of the regression equations for live conifer FRD versus mineral soil depth. This indicates that differences in mean FRD between structural stages varied with sampling year (Figure 1c, Table 4c), though this is likely due to the potentially erroneous high values from 2003. Both the linear and quadratic terms differed significantly with structural stages and sampling years, indicating

live conifer FRD depth distributions varied significantly with structural stage and sampling year (Figure 1c, Table 4c).

For mean ecto FRD in the LFH, there was a significant interaction between sampling year and structural stage (P=0.0790). The difference in the mean ecto FRD between 2003 and 2004 was least in the clearcut stands and increased with increasing stand age (Figure 1d). Mean ecto FRD was highest in the young forest stands in both sampling years, and especially so in the LFH (1.8 mg/cm^3) and shallow mineral soil in 2003. Mean ecto FRD was intermediate in the pole/sapling stand and lowest in the clearcut stand at all depths in both sampling years (Figure 1d). Mean ecto FRD was greater in the shallow mineral soil (D5) than in the LFH in the pole/sapling stands in 2004. The intercept, linear, and quadratic terms of the regression equations for ecto FRD versus mineral soil depth were all significantly different for structural stage, indicating mean ecto FRD and ecto FRD with depth (slope terms) varied significantly with structural stage (Figure 1d, Table 4d). Effects of sampling year and interaction of sampling year and stage were not significant. Across sampling years and depths, mean ecto FRD was highest in the young forest stand and lowest in the clearcut stand. The slope was much steeper in the young forest stand than in the pole/sapling stand and almost zero in the clearcut stand, while the decrease in slope was fastest in the young forest stand, and not significant in the clearcut stand (Figure 1d).

3.4 Fine Root Biomass

Total fine root biomass (FRB) ranged from 86 g/m^2 in the LFH of the clearcut stand in 2004 to 784 g/m^2 in the mineral soil of the pole/sapling stand in 2004 (Figure 2b). There was a significant interaction between structural stage and substrate (Table 5a). In the LFH, total FRB generally increased with stand structural stage in both 2003 and 2004 (Figure 2). However, in mineral soil total FRB was lowest in the clearcut stand, peaked in the pole/sapling stand, and was intermediate in the young forest stand (Table 6a, means followed by lower-case letters). There was a significant interaction between year and substrate (Table 5b). From 2003 to 2004, across all structural stages, total FRB generally increased in mineral soil, but decreased in the LFH (Figure 2).

FRB for the LFH and mineral soil combined ranged from 410 g/m^2 in the clearcut stand to 951 g/m^2 in the pole/sapling stand, with the young forest stand at an intermediate value of 756 g/m^2 (Table 6a). Combined total FRB differed significantly with structural stage (Table 7a), and mean FRB for the clearcut stand was significantly lower than that of both

Table 5. Summary of two-way repeated measures ANOVA investigating variance in mean total (T), live (L), live conifer (LC), and live conifer ectomycorrhizal (LCE) fine root biomass between clearcut, pole/sapling, and young Douglas-fir structural stages, organic and mineral substrates and years (2003 and 2004).

		Root Class							
		T		L		LC		LCE	
Source	**DF**	***F***	**P**	***F***	**P**	***F***	**P**	***F***	**P**
a) Between Subject Effects									
Stage	2	9.12	0.0018	4.86	0.0205	10.13	0.0011	16.61	<0.0001*
Substrate	1	41.52	<0.0001	22.07	0.0002	14.25	0.0014	2.07	0.1676
Stage × Substrate	2	4.68	0.0231*	2.64	0.0985	1.87	0.1823	0.58	0.5680
Error	18								
b) Within Subject Effects									
Year	1	0.54	0.4717	36.05	<0.0001	58.05	<0.0001	13.21	0.0019*
Year × Stage	2	0.59	0.5657	2.74	0.0918	8.83	0.0021	3.34	0.0582
Year × Substrate	1	8.09	0.0108*	1.76	0.2018	9.93	0.0055	0.12	0.7375
Year × Stage × Substrate	2	0.94	0.4086	4.17	0.0326*	6.34	0.0082*	0.93	0.4109
Error	18								

Note: *significance at α=0.05 for highest-order term in ANOVA.

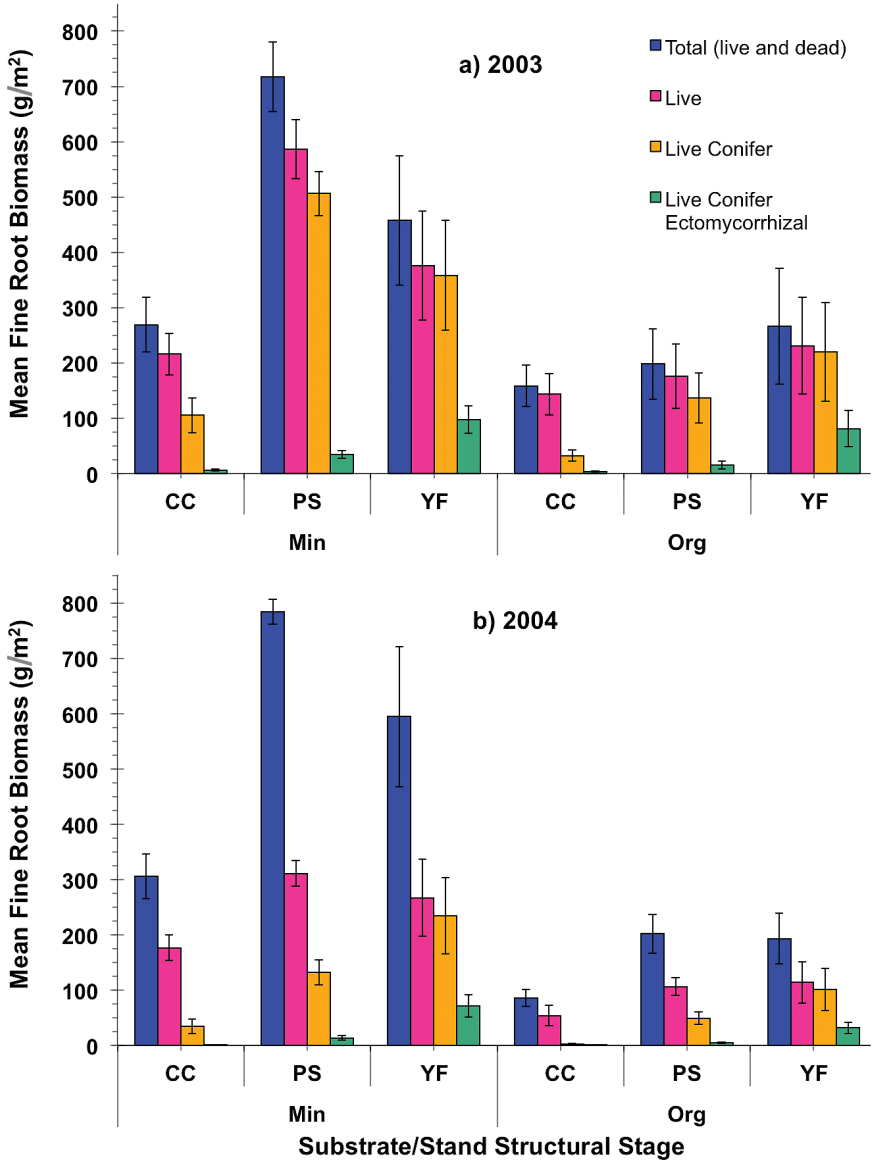

Figure 2. Mean (±1 S.E., n=4 per bar) fine root biomass (g/m^2) of four root classes for mineral and organic horizons in clearcut (CC), pole/sapling (PS), and young forest (YF) Douglas-fir stands on east-central Vancouver Island, BC, in 2003 and 2004.

the pole/sapling and the young forest stands, which were not significantly different from each other (Table 6a). Combined total FRB was not significantly different between sampling years (Table 7b, Figure 3).

Live FRB ranged from 59 g/m^2 in the LFH of the clearcut stand in 2004 to 586 g/m^2 in the mineral soil of the pole/sapling stand in 2003 (Figure 2). Live FRB was higher in 2003 than in 2004 for all structural stages and both substrates. In the LFH, live FRB increased with structural stage in both sampling years (Figure 2). There was a significant interaction between sampling year, structural stage, and substrate when partitioning variation in live FRB (Table 5b). In the LFH, live FRB increased gradually from clearcut stand to young forest stand, whereas in mineral soil it was lowest in the clearcut stand, highest in the pole/sapling stand (especially in 2003), and intermediate in the young forest stand (Figure 2).

Live FRB for the LFH and mineral soil combined ranged from 297 g/m^2 in the clearcut stand to 590 g/m^2 in the pole/sapling stand, with the young forest stand at an intermediate value of 494 g/m^2 (Table 6b). Combined live FRB was not significantly different between stages, however, it was significantly higher in 2003 than in 2004 (Table 7, Figure 3).

Live conifer FRB ranged from 2 g/m^2 in the LFH of the clearcut stand in 2004 to 506 g/m^2 in the mineral soil of the pole/sapling stand in 2003 (Figure 2). There was a significant

Table 6. Mean (± 1 S.E.) total, live, live conifer, and live conifer ectomycorrhizal fine root biomass (g/m^2) for organic (LFH) and mineral substrates in clearcut (CC), pole/sapling (PS), and young forest (YF) Douglas-fir stands across years (2003 and 2004).

	Stand Structural Stage							
Substrate	**CC**		**PS**		**YF**		**ALL**	
a) Total								
Mineral	287.42 ab*	(30.43)	750.75 c	(33.32)	525.98 ac	(83.91)	521.39	(49.77)
LFH	122.24 d	(23.23)	199.79 bd	(33.68)	229.89 abd	(54.86)	183.98	(23.76)
Combined	409.66 A	(36.02)	950.54 B	(55.72)	755.88 B	(115.49)	705.36	(63.05)
b) Live								
Mineral	196.18	(21.64)	448.73	(58.56)	321.45	(59.56)	322.12	(34.89)
LFH	100.95	(24.96)	141.51	(30.81)	172.46	(49.17)	138.31	(21.03)
Combined	297.12	(35.64)	590.24	(83.38)	493.92	(97.01)	460.43	(49.35)
c) Live Conifer								
Mineral	69.74	(20.81)	319.04	(73.79)	296.42	(60.76)	228.40	(39.01)
LFH	17.25	(7.38)	92.97	(27.13)	160.33	(50.35)	90.19	(22.04)
Combined	87.00	(25.97)	412.01	(95.78)	456.75	(101.31)	318.58	(56.75)
d) Live Conifer Ectomycorrhizal								
Mineral	3.06	(1.44)	24.10	(5.59)	84.67	(15.69)	37.27	(8.97)
LFH	1.65	(0.73)	9.95	(3.91)	56.37	(18.55)	22.66	(7.86)
Combined	4.72 A	(1.87)	34.04 A	(9.15)	141.03 B	(31.69)	59.93	(16.12)

Note: *for root classes and substrates where no main effect or interaction with year occurred (Tables 5 and 7), SNK mean separations were calculated. Lower case letters indicate mean separations for individual substrates, while upper case letters indicate mean separations for combined substrates (LFH plus mineral soil to 55 cm). Means followed by the same letters are not significantly different.

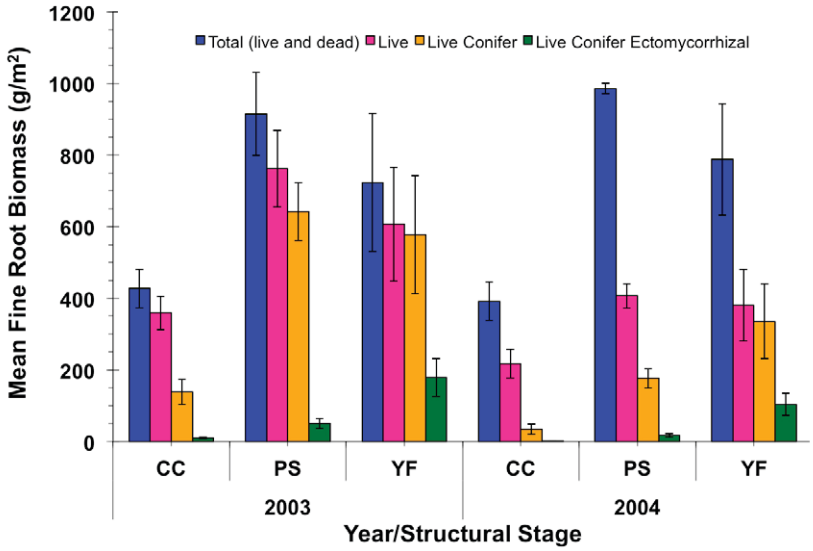

Figure 3. Mean (± 1 S.E.; n=4 per bar) fine root biomass (g/m^2) of four root classes for combined organic (LFH) and entire mineral profiles in clearcut (CC), pole/sapling (PS), and young forest (YF) Douglas-fir stands on east–central Vancouver Island, BC, Canada in 2003 and 2004.

Table 7. Summary of repeated measures two-way ANOVA investigating differences in mean total (T), live (L), live conifer (LC), and live conifer ectomycorrhizal (LCE) fine root biomass between clearcut, pole/sapling, and young forest Douglas-fir stand structural stages for the combined LFH and entire mineral soil profile for 2003 and 2004.

		Root Class							
		T		L		LC		LCE	
Source	DF	*F*	P	*F*	P	*F*	P	*F*	P
a) Between Subject Effects									
Stage	2	6.19	0.0204*	3.15	0.0919	6.15	0.0207	8.90	0.0074*
Error	9								
b) Within Subject Effects									
Year	1	0.58	0.4640	26.78	0.0006*	44.94	<0.0001	13.33	0.0053*
Year × Stage	2	0.64	0.5514	2.03	0.1869	6.83	0.0157*	3.38	0.0806
Error	9								

Note: *indicates significance at α=0.05 for highest-order term in the ANOVA.

interaction between sampling year, structural stage, and substrate when partitioning variation in live conifer FRB (Table 5b). In the LFH in 2003 and 2004 and the mineral soil in 2004, live conifer FRB increased gradually through the structural stages; however, in the mineral soil in 2003, it was lowest in the clearcut stand, highest in the pole/sapling stand, and intermediate in the young forest stand (Figure 2).

Live conifer FRB for the LFH and mineral soil combined ranged from 87 g/m^2 in the clearcut stand to 412 g/m^2 in the pole/sapling stand and 457 g/m^2 in the young forest stand (Table 6c). There was a significant interaction between sampling year and structural stage when partitioning variation in combined live conifer FRB (Table 7b). Combined live conifer FRB was highest in the pole/sapling stand in 2003, whereas in 2004 FRB increased with increasing structural stage: it was lowest in the clearcut stand and highest in the young forest stand (Figure 3).

Live conifer ectomycorrhizal (ecto) FRB ranged from 0.04 g/m^2 in the LFH of the clearcut stand in 2004 to 98 g/m^2 in the mineral soil of the young forest stand in 2003 (Figure 2). Mean ecto FRB differed significantly with structural stage for both years, and was significantly higher in 2003 than in 2004 (Table 5). For all substrates, the mean ecto FRB was significantly higher in the young forest stand than in either the pole/sapling or the clearcut stands, which were not significantly different from each other (not shown).

Ecto FRB for the LFH and mineral soil combined ranged from 5 g/m^2 in the clearcut stand to 34 g/m^2 in the pole/sapling stand, and was 141 g/m^2 in the young forest stand (Table 6d). Combined ecto FRB differed significantly with structural stage (Table 7a), and in both years was higher in the young forest stand than in either the pole/sapling or the clearcut stands, which were not significantly different from each other (Table 6d). Combined ecto FRB was significantly higher in 2003 than in 2004 (Table 7b, Figure 3).

4. Discussion

4.1 Fine Root Carbon Concentration

While investigators commonly use 50% as a standard concentration for carbon (C) in plant material such as fine roots (Howard et al. 2004; Smith et al. 2002), it is important to verify this value because systematic errors can undermine the accuracy of carbon mass estimates when scaling is undertaken over large areas. Results from this study show that fine root %C in the mineral soil layers differed with stand structural stages. Overall, observations of fine root %C ranged from 1.6 to 5.4% less than 50%, implying that fine root carbon mass could be overestimated by up to 400 kg C/ha in the pole/sapling stand, by 120 kg C/ha in the young forest stand, and by 45 kg C/ha in the clearcut stand, if fine root C was assumed to be 50% (see Table 6 and %C results). Such discrepancies should be noted in carbon budget models, and when calculating carbon sequestration.

Possible reasons for the lower fine root %C include differences in vegetation type (woody tissue has a higher %C than non-woody tissue), amount of mineral particles adhering to fine roots (which can "dilute" measured %C), and degree

of mycorrhizal development. The abundant shrub and herb roots in the pole/sapling samples may be responsible for the low root %C observed in that stage.

Across all structural stages, fine root %C was significantly lower in the shallowest mineral horizon (D5) than in the LFH and deeper mineral layers. The shallow mineral soil is where intensive fine rooting occurs (Grier et al. 1981; Janssens et al. 1999; Persson 1980; Reynolds 1970; Vogt et al. 1981, 1980), and where mycorrhizal density is high (Fogel and Hunt 1979; McMinn 1963; Olsthoorn and Tiktak 1991; Sylvia and Jarstfer 1997). Differences in fine root %C between D5 and all other horizons may be due to indirect effects of differences in nutrient content between the horizons (Kimmins and Hawkes 1978; Sainju and Good 1993), which may increase the mycorrhizal fine root density of the soil layer below the litter layer (McMinn 1963; Olsthoorn and Tiktak 1991; Sylvia and Jarstfer 1997). Nutrients in the LFH and upper mineral soil are primarily in organic forms—these are unavailable to roots, but potentially available to mycorrhizae, which have the demonstrated ability to take up organic nitrogen compounds (Trofymow and van den Driescche 1991). A large fraction of ectomycorrhizal roots is composed of fungal mantle tissue and, thus, may have less of the C-rich phenolic compounds and tannins than non-mycorrhizal roots have. This would reduce the root %C in horizons that have many mycorrhizal roots.

To test if the low %C observed in fine roots at the shallowest mineral substrate was due to "dilution" of those samples by mineral soil particles adhering to abundant root hairs on some roots, or to inherent differences between root types, we carefully cleaned small subsamples of different root categories from 2004 to remove all mineral material. Fine roots in shallow mineral soil had a %C (47.1 %C) that was almost 3% lower than that of fine roots in the LFH (49.9 %C), which may be a result of clay particles embedded within the fungal mantle of roots in the mineral soil. Live conifer ectomycorrhizal fine root %C (47.5 %C) was around 2% lower than either live non-coniferous (49.9 %C) or live coniferous non-ectomycorrhizal (49.6 %C) fine roots. Consequently, our results suggest that the low %C of fine roots in shallow mineral soil may be due to the large amount of ectomycorrhizal roots in that horizon, which have lower %C than non-ectomycorrhizal roots, and not to adhering soil particles.

4.2 Fine Root Density Distribution

For all stands investigated, fine root density was highest in the organic LFH layer and decreased rapidly with increasing soil depth. This result generally agrees with those of Santantonio and Hermann (1985) and Reynolds (1970), and those of Kurz and Kimmins (1987), who investigated second-growth Douglas-fir stands on eastern Vancouver Island. Similar trends have also been observed for other species in various geographical areas (Janssens et al. 1999; Kimmins and Hawkes 1978; Sainju and Good 1993; Squire et al. 1978; Sylvia and Jarstfer 1997).

Certain structural stages in our study exhibited higher fine root densities in the shallowest mineral soil layer (D5) than in the organic LFH layer (D0), and this has also been reported by others (Grier et al. 1981; Janssens et al. 1999; Persson 1980; Reynolds 1970; Vogt et al. 1981, 1980). A thin organic layer in one of the pole/sapling plots could have contributed to the low fine root density values in that stand by assuming that a shallow LFH layer dries out more quickly, inhibiting root growth and accelerating root death, as reported by Kurz and Kimmins (1987).

The highest densities of ectomycorrhizal roots were found in the organic LFH layer, or in the mineral horizon just below it, and density decreased in deeper horizons. This result is consistent with those of Sylvia and Jarstfer (1997), who observed a decrease in mycorrhizal density with increasing soil depth in a pine plantation in Florida. Olsthoorn and Tiktak (1991) report much higher numbers of mycorrhizal root tips from 0 to 20 cm deep than for deeper horizons (down to 85 cm) for Douglas-fir stands in Holland.

4.3 Fine Root Biomass and Stand Age

Fine root biomass (FRB) results from this study are comparable to those at the upper end of the biomass ranges reported in the literature for similar-aged stands (Table 8).

The lack of conifer fine roots in the clearcut stand is undoubtedly due to the young age and small size of the regenerating trees, although the rocky soil texture (Table 1) and distinct lack of a well-developed LFH layer may also be contributing factors. A lack of published results for clearcut or very young stands in the literature, and an abundance of results for old-growth stands, makes comparisons with our results difficult. Vogt et al. (1983b) report low total and live conifer FRB values in clearcut stands. In agreement with our findings for the 14- and 54-year-old (young forest) stands, Vogt et al. (1983a, 1983b) report that live conifer fine root biomass increased with increasing stand age for Douglas-fir stands between 11 and 49 years old in western Washington. Conversely, Vogt et al. (1987) detected no difference in total fine root biomass between different-aged Douglas-fir stands within the same productivity class.

The results of Vogt et al. (1983b) for a chronosequence of 20 Douglas-fir stands in western Washington are very similar to ours. For high-productivity stands, they found an increase in live fine root biomass in the forest floor from clearcut and 33- to 49-year old stands, but in mineral soil they observed a peak in biomass for 11- to 14-year-old stands, with a subsequent decline for 33- to 49-year-old stands. The total FRB and live

Table 8. Comparison of mean fine root biomass (g/m^2) from published literature and this study.

Source	Stand Type	Variable Measured	Mean (±1 S.E.) (g/m^2)	Notes
This study	3- to 54-year-old Douglas-fir on east–central Vancouver Island, BC	Total fine root (< 2 mm diam.) biomass	409.66 (36.02)–950.54 (55.72) Mean: 705.36 (63.05)	Soil sampled to 55 cm
This study	3- to 54-year-old Douglas-fir on east–central Vancouver Island, BC	Live fine root (< 2 mm diam.) biomass	297.12 (35.64)–590.24 (83.38) Mean: 460.43 (49.35)	Soil sampled to 55 cm
Keyes and Grier (1981)	40-year-old Douglas-fir in western Washington, USA	Fine root (≤ 2 mm diam.) biomass (assumed total)	270–830	Soil sampled to 45 cm. Value is seasonal maximum.
Kurz and Kimmins (1987)	33- to 71-year-old Douglas-fir on Vancouver Island, BC	Live fine root (< 2 mm diam.) biomass	182.0 (17.6)–791.5 (56.2)	Soil sampled to 50 cm. Lowest biomass in oldest stand.
Lee et al. (2004)	290- to 400-year-old Douglas-fir in the Olympic Mountains, Washington, USA	Fine root (≤ 2 mm diam.) biomass (assumed total)	Between 600 and 1100	Soil sampled to 80 cm
Santantonio et al. (1977)	450-year-old Douglas-fir	Fine root (< 5 mm diam.) biomass (assumed total)	970	Soil cored around Douglas-fir trees
Vogt et al. (1983a)	11- to 49-year-old Douglas-fir in western Washington, USA	Live conifer fine root (≤ 2 mm diam.) biomass	20.9–593.0	Forest floor sampled only
Vogt et al. (1983a)	11- to 49-year-old Douglas-fir in western Washington, USA	Live conifer mycorrhizal fine root (≤ 2 mm diam.) biomass	2.3 (1.6)–85.6 (19.3)	Forest floor sampled only
Vogt et al. (1987)	11- to 49-year-old Douglas-fir in western Washington, USA	Total fine root (< 2 mm diam.) biomass	103.3 (29.6)–735.5 (197.4)	Soil sampled to 15 cm
Vogt et al. (1983b)	Clearcut to 163-year-old Douglas-fir in western Washington, USA	Total fine root (≤ 2 mm diam.) biomass	57–444 high productivity site 60–687 low productivity site	Soil sampled to 15 cm
Vogt et al. (1983b)	Clearcut to 163-year-old Douglas-fir in western Washington, USA	Live fine root (≤ 2 mm diam.) biomass	19–166 high productivity site 20–261 low productivity site	Soil sampled to 15 cm

FRB values in our study were higher than theirs (Table 8), but they only sampled the soil to a depth of 15 cm, whereas we sampled to at least 45 cm. However, the trends in the data are remarkably alike and are more readily apparent because of the similar age classes sampled.

Overall, the young forest stand had lower total FRB than the pole/sapling stand, but much higher ecto FRB. When looking at substrate, the young forest stand showed a higher total FRB than the pole/sapling stand in the LFH, but the opposite in the mineral soil, where nutrients may be more depleted in the older stand. Trees in the pole/sapling stand may still be in the process of exploiting the mineral horizons for nutrients and growing space with longer-lived, non-mycorrhizal fine roots. When canopy closure is reached, a stabilization of fine

root biomass eventually occurs (Vogt et al. 1983b). As a stand matures, the mineral soil is gradually depleted of nutrients, and a shift in intensive fine rooting seems to occur: fine rooting becomes more concentrated in the organic/upper mineral soil layers, and a shift in the type of fine root produced seems to occur as well (Finér et al. 1997; Santantonio et al. 1977).

The difference between the live and live conifer fine root biomass in 2004 (the live conifer root values for 2003 were not used as they are potentially erroneous) in the pole/sapling and young forest stands (Figure 3b) indicates that a greater fraction of the live and total FRB in the pole/sapling stand is from shrubs and herbs. The pole/sapling stand had more abundant aboveground shrub and herb biomass (400–600 g/m^2) than the young forest stand (50–70 g/m^2).

4.4 Contributions of Ectomycorrhizal Roots to Fine Root Biomass

We found that the percentage of ecto to live conifer fine root biomass was consistently much higher in the young forest stand (31%) than in the pole/sapling stand (9%) for the LFH, mineral soil, and both combined for both years. These results suggest that in the young forest stand, trees allocate a greater proportion of carbon to ephemeral but efficient absorptive structures— mycorrhizal fine roots—than they do in the pole/sapling stand. This contrasts with the findings of Vogt et al. (1981), who report no apparent differences in the ratio of mycorrhizal to fibrous fine roots between 23- and 180-year-old subalpine *Abies amabilis* stands in western Washington. However, the percentage of ecto to live conifer FRB we observed for 14-year-old Douglas-fir stands (9% for mineral and organic LFH horizons combined) is similar to their results for the 23-year-old stand in spring.

For mineral and organic (LFH) substrates, ecto FRB was lowest in the clearcut stand and highest in the young forest stand. For each structural stage, it was higher in the organic than in the mineral layer. These results agree with those of Vogt et al. (1980, 1981, 1983a) who found higher live mycorrhizal fine root biomass in 45- to 49-year-old Douglas-fir stands than in 11- to 14-year-old stands. Outerbridge et al. (2009) found the percentage of ectomycorrhizal colonization of conifer tree roots in regenerating stands 25–45 m from adjacent mature (>90-year-old) stands was least in 5–8-year-old stands, intermediate in 27-year-old stands, and highest in 57-year-old stands. Greater ectomycorrhizal colonization and species richness in the organic layer than in mineral soil has also been reported for mature and old-growth Douglas-fir stands on south–eastern Vancouver Island (Goodman and Trofymow 1998). One potential reason for the higher fine root and mycorrhizal biomass in older stands is the increased thickness of the organic layer with increasing stand age (Finér et al. 1997; Grier et al. 1981). We could not corroborate those results for the Douglas-fir stands we studied, since LFH thickness did not significantly differ with structural stage.

4.5 Effects of LFH Thickness on Fine Root Biomass

Differences in the thickness of the LFH layer varied between sampling years and structural stages, and there was a lot of variation in the data. In the LFH, fine root density, which is normalized by the LFH thickness, exhibited differences primarily due to sampling year or structural stage. LFH thickness showed an interaction between sampling year and structural stage. This in turn caused an interaction between sampling year and structural stage for fine root biomass. When comparing biomass values in Figure 2 with LFH thicknesses in Table 2 (biomass divided by LFH thickness is fine root density), it is clear that the thin LFH in the pole/sapling stand in 2003 and the clearcut stand in 2004 increased fine root density, resulting in similar trends between structural stages in both sampling years, with higher values in 2003.

4.6 Difference Between Sampling Years in Fine Root Biomass

Across all structural stages, total fine root biomass was generally higher in 2004 than in 2003; however, all live root class values were much lower in 2004. In other words, there were more dead roots in 2004 than in 2003. The spring and early summer in 2003 were mild with good rainfall. However, microclimatic data from the clearcut stands showed that the summer dry spell started in June in 2003, compared to July for the two previous years (Humphreys et al. 2005). Soil water potential can decrease earlier in the summer in older forested stands compared to regenerating stands (Benton 1998). The occurrence of this favourable period early in the 2003 growing season could have resulted in above-average fine root production, and the early summer dry season in 2003 may have killed off a large portion of those fine roots (Gower et al. 1992). These conditions may account for the decrease in live fine root biomass observed in the 2004 sample.

5. Conclusions

Differences in fine root %C between forest stand structural stages, soil depths, and ectomycorrhizal and non-ectomycorrhizal roots should be considered when converting fine root biomass to carbon mass. Using a value of 50% may overestimate carbon contributions of fine roots to carbon budgets or other models.

Density of all fine root classes in the LFH generally increased with stand age or structural stage and decreased with increasing depth in mineral soil. Unexpectedly, total, live, and live conifer fine root density was generally highest in the pole/sapling stand, not in the young forest stand. Ectomycorrhizal fine root density was significantly higher in the young forest than in the pole/sapling or clearcut stands, and especially high in the LFH and shallow mineral soil.

Total fine root biomass generally increased with structural stage in the LFH, but the effects of stage differed in mineral soil. For the combined LFH and mineral soil, total fine root biomass was lowest in the clearcut stand and highest in the pole/sapling and young forest stands. Live and ectomycorrhizal fine root biomass values were lower in 2004 than 2003, which may have resulted from a dry summer in 2003 causing root death. Ectomycorrhizal fine root biomass was significantly higher in the young forest stand than in both the pole/sapling and clearcut stands. The higher fine root biomass in the pole/sapling stand was unexpected; however, the higher ectomycorrhizal root biomass in the young forest suggests that a greater proportion of carbon is allocated to ephemeral but efficient nutrient absorptive structures in forests at that stage of development.

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