

Vertical fine root distributions of western redcedar, western hemlock, and salal in old-growth cedar-hemlock forests on northern Vancouver Island

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Abstract: The vertical distributions of fine roots of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) western redcedar (*Thuja plicata* Donn ex D. Don), and salal (*Gaultheria shallon* Pursh) were characterized in old-growth cedar-hemlock forests on northern Vancouver Island. Total biomasses of cedar, hemlock, and salal roots in the forest floor and upper mineral soil were 817, 620, and 187 g·m⁻², respectively. Hemlock and salal fine roots were concentrated in the upper forest floor, while cedar fine roots were evenly distributed through the profile. Salal and hemlock fine root densities (g·m⁻³) in the forest floor and mineral soil were positively correlated, as were salal and cedar root biomass distributions (g·m⁻²). Only salal and hemlock root densities were significantly correlated with N concentrations. Hemlock root densities were negatively correlated with total N, and salal root densities were negatively correlated with total N and soluble organic N. Based on fine root densities, hemlock and salal probably compete for resources in the upper forest floor, whereas cedar accesses resources in the lower organic and mineral soil horizons. The differences in the vertical distributions of cedar, hemlock, and salal fine roots may partly explain the co-occurrence and different productivities of the three species in cedar-hemlock forests.

Résumé : La distribution verticale des racines fines de la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.), du thuya géant (*Thuja plicata* Donn ex D. Don) et du salal (*Gaultheria shallon* Pursh) a été caractérisée dans les forêts anciennes de thuya et de pruche du Nord de l'île de Vancouver. La biomasse totale des racines du thuya, de la pruche et du salal dans la couverture morte et la partie supérieure du sol minéral atteint respectivement 817, 620 et 187 g·m⁻². Les racines fines de la pruche et du salal sont concentrées dans la partie supérieure de la couverture morte tandis que les racines fines du thuya sont uniformément réparties dans le profil de sol. La densité des racines fines (g·m⁻³) du salal et de celles de la pruche sont positivement corrélées dans la couverture morte et le sol minéral, de même que la distribution de la biomasse des racines (g·m⁻²) dans le cas du salal et du thuya. Seules la densité des racines du salal et de celles de la pruche sont significativement corrélées avec la concentration de N. La densité des racines de la pruche est négativement corrélée avec la quantité totale de N; la densité des racines du salal est négativement corrélée avec la quantité totale de N et la quantité de N organique soluble. Sur la base de la densité des racines fines, la pruche et le salal compétitionnent probablement pour les ressources dans la partie supérieure de la couverture morte tandis que le thuya a accès aux ressources de l'horizon organique et du sol minéral situés au-dessous. Les différences dans la distribution verticale des racines fines du thuya, de la pruche et du salal peuvent en partie expliquer la coexistence et la différence de productivité des trois espèces dans les forêts de thuya et de pruche.

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Introduction

Fine roots are responsible for most nutrient and water uptake by plants (Bowen 1984; Landsberg and Gower 1997)

and so are important in determining the productivity and growth of plants in terrestrial ecosystems. In forests, fine roots of different species often overlap, occupying the same organic or mineral soil horizons (Jonsson et al. 1988). However, various degrees of vertical and horizontal separation in fine root location have also been found (Grier et al. 1981; Persson 1983; Strong and La Roi 1983b; Gholz et al. 1986; Manning and Barbour 1988), and such distinctions in the distributions of fine roots may allow for spatial separation of resource acquisition, thereby reducing competition (Yeaton et al. 1977; Manning and Barbour 1988; Franco and Nobel 1990). Thus, it has been hypothesized that the co-occurrence of plants limited by the same resources may be facilitated through accessing resources in different soil horizons or locations (Berendse 1979; Fitter 1982; McKane et al. 1990; Schulze et al. 1994; Nadelhoffer et al. 1996) and that the plant species with more distinct fine root distributions may

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have higher productivities than those with overlapping root systems (Yeaton et al. 1977; Manning and Barbour 1988; Fredericksen and Zedaker 1995).

Cedar-hemlock (CH) forests on northern Vancouver Island, British Columbia, are predominantly composed of western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and salal (*Gaultheria shallon* Pursh), which show different levels of productivity. Salal re-occupies more than 50% of available ground space within 8 years of clearing and burning CH sites (Messier and Kimmins 1991) and forms a dense understory in old-growth forests. Of the two conifers, cedar displays higher growth and, on 10-year-old regenerating CH cutovers, has a mean annual increment (MAI) of 5.25 m²·ha⁻¹·year⁻¹ compared with hemlock, which has a MAI of 1.47 m²·ha⁻¹·year⁻¹. Nitrogen availability on CH sites is extremely low about 5–8 years after clear-cutting and burning (Messier 1993), and fertilizer trials have established that N limits conifer growth in these forests (Weetman et al. 1989). Thus, the co-existence and different productivities of cedar, hemlock, and salal growing in N-limited CH forests may be the result of spatial separation of access to N. Differences in the vertical distributions of fine roots of the three species may allow them to acquire N from different forest floor and soil horizons.

To test the hypothesis that cedar, hemlock, and salal have different fine root distributions in CH forests, fine root densities and biomass in the forest floor and upper mineral soil horizons of three old-growth forest sites were characterized. Nitrogen concentrations and contents in the horizons were also measured to determine if the arrangements of cedar, hemlock, and salal fine roots were correlated with the distributions of different N forms. The main questions addressed were as follows. Do the three species differ in their fine root density and biomass distribution patterns? Are root and N distributions correlated? Could species-specific fine root distribution patterns, in part, explain the differences in the productivities of cedar, hemlock, and salal in CH forests?

Materials and methods

Site description

Forest floor and mineral soil samples were collected from three old-growth CH forests in Western Forest Product Ltd. Tree Farm License (TFL) 6 on northern Vancouver Island, British Columbia. These sites are located within the very wet maritime Coastal Western Hemlock (CWHvm1) biogeoclimatic zone (Green and Klinka 1994) and receive an average annual precipitation of 1700 mm, 65% of which falls between October and February. The mean annual temperature is 7.9°C, with a daily mean range from 2.4°C (January) to 13°C (August) (Prescott and Weetman 1994).

Western redcedar dominates the main canopy of old-growth CH forests, and western hemlock is typically found in the co-dominant, intermediate, and suppressed layers. The understory is primarily composed of salal, with minor components of *Vaccinium* spp., deer fern (*Blechnum spicant* (L.) Roth), bunchberry (*Cornus canadensis* L.), salmonberry (*Rubus spectabilis* Pursh), and the mosses *Hylocomium splendens* (Hedw.) B.S.G., *Kindbergia oregana* (Sull.) Ochyra, and *Rhytidiadelphus loreus* (Hedw.) Warnst. (deMontigny 1992). Thick forest floors, which are classified

as Humimors (with well developed H horizons) or Lignomors (with large amounts of decomposing wood in the H horizon) (Green et al. 1993), overlay duric or orthic Humo-Ferric Podzols (Prescott and Weetman 1994). The soil parent materials are mainly sandy loam glacial tills with smaller areas of glacial fluvial, fluvial terrace, or finer textured saprolites (Lewis 1985).

Root sample collection

At each CH forest site, seven or eight potential sampling locations were chosen according to specific criteria. There had to be at least one stem of hemlock, cedar, and salal plant within 5 m and no other tree species or shrub greater than 1 m in height within 5 or 2 m of the spot, respectively. From the seven or eight potential locations, five were randomly selected, and at each point a pit at least 0.75 m wide and 1 m long was dug to the depth of the hard pan layer. In all pits, this impervious layer was deeper than 10 cm into the mineral soil. The thicknesses of the F, Hr, and Hh forest floor horizons (Green et al. 1993) were measured to the nearest 0.5 cm on the exposed profile faces. Vertical monoliths of forest floor and mineral samples (15 × 15 cm) were collected from the profile and separated into four horizons (F, Hr, Hh, and Ae/B). The F horizon is on the surface under freshly deposited litter and consists of partially decomposed plant residues. The Hr is typically below the F layer and contains residues that are in a more advanced stage of decomposition, but some plant litter fragments are still recognizable. The Hh horizon is the most heavily decomposed horizon and is below the Hr, if present. The entire depths of the F and Hr horizons were included in the samples. In Hh horizons more than 15 cm deep, only the top 15 cm was collected, and in mineral soil, only the upper 10 cm was sampled. There were very few roots below 10 cm in the mineral soil. When decaying wood was encountered in a horizon, an alternate sampling location in the pit was randomly chosen. The mineral soil samples included both Ae and B horizons. This sampling method was chosen over the soil coring method because of the sampling depths (up to 93 cm) and to avoid decomposing wood, large tree roots, and rocks.

Root separation and cleaning

The forest floor and mineral soil samples were transported back to the University of British Columbia (UBC), and maintained at 4°C until processed. In the laboratory, each sample was weighed, hand sorted to remove all visible roots, and then successively sieved through 5 and 2 mm mesh pores to remove the remaining root fragments. The mineral soil samples were only passed through 5 mm mesh sieves; the coarse fragments (>5 mm) remaining on the sieve were weighed, and the volumes were determined by water displacement. These volumes were subtracted from the sample volumes.

Following separation from the forest floor or mineral soil, the roots were carefully rinsed with tap water. Care was taken to recover as many root fragments as possible during the sorting process. The samples could not be wet-sorted, because the sieved forest floors and mineral soils were also used for the N analyses. All roots less than 1 cm in diameter were considered components of the forest floor and mineral

soil and, therefore, were included in the forest floor and soil masses to estimate bulk densities.

During the rinsing process the roots were sorted according to species and status (live or dead). The three species were easy to distinguish because of their different root morphologies. Hemlock has a distinct ectomycorrhizal branching pattern, and many of the roots were covered in fungal mantles. Cedar, which forms vesicular-arbuscular (VA) mycorrhizae, has thicker, paler roots with long laterals, and salal roots are white and very thin (Xiao 1994), which is a root morphology characteristic of the Ericaceae (Ehrenfeld et al. 1992). The criteria used to determine live or dead status included root condition and colour (Persson 1983; Tufekcioglu et al. 1999). If the roots were pliable and the cortex was still white, they were considered to be alive or recently dead.

The "live" fraction of roots were dried to constant mass at 70°C and divided into two size classes based on fresh mass diameters: fine roots (≤ 2 mm) and coarse (> 2 mm) roots. Conversion factors were determined with the diameters of 20 fine roots of each species measured before and after drying at 70°C. Variability in diameter loss with drying was very low, and the standard errors were never larger than 2% of the means. Therefore, the root samples sorted after drying probably provided accurate estimates of cedar, hemlock, and salal fine root biomass. Only the fine roots were weighed and included in the analyses. All roots were processed and dried within 11 days of collection. The root measurements were expressed as volume ($\text{g}\cdot\text{m}^{-3}$) and total biomass ($\text{g}\cdot\text{m}^{-2}$) in each horizon to provide estimates of fine root density and biomass distributions, respectively.

Forest floor and mineral soil N assessments

Following the removal of roots and sieving, the forest floor and mineral soil samples were assessed for concentrations of total N, extractable NO_3^- -N and NH_4^+ -N, and soluble organic N (SON). Forest floor and soil samples were dried to constant mass at 70°C, and the forest floors were ground in a Wiley mill (No. 40 sieve). Equivalent masses (5 g) of each forest floor and soil were then composited by site and horizon, resulting in 12 samples (4 horizons \times 3 sites). Total N was measured on the composited samples as total Kjeldahl nitrogen (TKN) (Bremner and Mulvaney 1982) at the Soil Science Laboratory of UBC. To estimate extractable NO_3^- and NH_4^+ and SON concentrations, 5 g of each forest floor or mineral soil sample (not composited) was shaken with 50 mL of 2 M KCl for 1 h. The extracts were then composited by site and horizon and were filtered through pre-soaked (2 M KCl) Whatman No. 42 filter paper, followed by filter sterilization through Gelman 0.45- μm micropore syringe attachments. Nitrate-N and NH_4^+ -N concentrations were measured by flow injection using a Lachat autoanalyzer. SON concentrations were determined using a modified version of the persulphate oxidation technique (Cabrera and Beare 1993). Briefly, 10 mL of persulphate solution (15 g NaOH, 40 g low-N $\text{K}_2\text{S}_2\text{O}_8$, and 15 g boric acid dissolved in 1 L deionized water) was added to 5-mL subsamples of extract, and the mixtures were autoclaved at 121°C for 45 min. After autoclaving, the samples were diluted with 5 mL of deionized water prior to flow-injection analysis for NO_3^- -N. Soluble organic N was calculated as

the difference between NO_3^- -N measured following persulphate oxidation and inorganic N (NO_3^- -N and NH_4^+ -N) measured in the non-autoclaved samples. Extractable NO_3^- and NH_4^+ , and SON analyses were conducted at the Engineering Laboratory at UBC. All drying and extractions were completed within 5 days of sample collection.

Statistical analyses

The N contents and fine root abundances in each horizon were analyzed by N form and species as completely randomized block designs, blocked by forest site. Measurements from each pit within a forest site were treated as subsamples. The N values were expressed as concentrations ($\text{g}\cdot\text{m}^{-3}$) and contents ($\text{g}\cdot\text{m}^{-2}$), and the roots were expressed as volumetric densities ($\text{g}\cdot\text{m}^{-3}$) (Ehrenfeld et al. 1992) and masses ($\text{g}\cdot\text{m}^{-2}$). Differences in these mean values from each horizon were determined with analysis of variance (ANOVA) using the general linear model (GLM) procedure of SAS, followed by Bonferroni pairwise test comparisons of the least square means. The alpha level (0.05) was adjusted for the number of comparisons using Bonferroni's adjustment (Neter et al. 1996). Block \times horizon interactions were tested using the sampling errors for the cedar, hemlock, and salal root analyses. The Tukey test for non-additivity was used to determine significant site \times horizon interactions in the N concentrations and contents, because the extracts were composited at each site (Steel and Torrie 1960). All the root measurements required transformation prior to analysis. The cedar and hemlock root densities ($\text{g}\cdot\text{m}^{-3}$) and the cedar and salal total root biomasses ($\text{g}\cdot\text{m}^{-2}$) were $\log(x + 1)$ transformed. Square-root transformations were applied to the salal root densities and hemlock total biomass measurements. Back-transformed means are reported in the tables and figures.

Relationships between N (total N, NO_3^- , NH_4^+ , and SON) concentrations and cedar, hemlock, and salal fine root densities ($\text{g}\cdot\text{m}^{-3}$) in each horizon were explored with Spearman rank correlations (Conover 1980). Spearman rank correlations were also calculated among the vertical fine root distributions of cedar, hemlock and salal, using root values from each pit. An alpha level of 0.05 was also applied to the correlation analyses. All analyses were conducted with SAS (SAS Institute Inc. 1993).

Results

In the three old-growth CH forests, the Hh was the thickest forest floor horizon with a mean depth of 0.31 m (Table 1). The Hh horizon also had the greatest mean bulk density ($120 \text{ kg}\cdot\text{m}^{-3}$) and total mass ($368 \text{ Mg}\cdot\text{ha}^{-1}$). The F layer was consistently the thinnest horizon (mean 3 cm), and had the lowest mean density ($73 \text{ kg}\cdot\text{m}^{-3}$) and total mass ($23 \text{ Mg}\cdot\text{ha}^{-1}$). The entire forest floor averaged 0.46 m in thickness, with a total mass of $485 \text{ Mg}\cdot\text{ha}^{-1}$. The bulk densities of the upper 10 cm mineral soils were much greater than those of the forest floors ($690 \pm 125 \text{ kg}\cdot\text{m}^{-3}$ at site 1, $373 \pm 84 \text{ kg}\cdot\text{m}^{-3}$ at site 2, and $682 \pm 52 \text{ kg}\cdot\text{m}^{-3}$ at site 3).

The forest floor and soil contained a mean of $6115 \text{ kg}\cdot\text{ha}^{-1}$ of total N. Of this, $84 \text{ kg}\cdot\text{ha}^{-1}$ was SON, $1.0 \text{ kg}\cdot\text{ha}^{-1}$ was NH_4^+ -N, and $0.05 \text{ kg}\cdot\text{ha}^{-1}$ was NO_3^- -N (Table 2). On a volume basis ($\text{g}\cdot\text{m}^{-3}$), there were no significant differences in the concentrations of SON, NO_3^- , NH_4^+ , and total N among

Table 1. Characteristics of the forest floor horizons in the three old-growth CH forests.

Site and horizon	Mean thickness (m)	Thickness range (m)	Bulk density (kg·m ⁻³)	Mass (Mg·ha ⁻¹)
Site 1				
F	0.03 (0.001)	0.02–0.04	69.64 (6.26)	20.89 (2.20)
Hr	0.13 (0.03)	0.10–0.18	75.39 (5.73)	95.49 (20.10)
Hh	0.39 (0.16)	0.07–0.60	112.52 (29.25)	438.84 (182.94)
Total forest floor	0.47 (0.09)	0.28–0.73	—	552.91 (162.48)
Site 2				
F	0.04 (0.001)	0.03–0.04	73.10 (6.00)	26.32 (1.79)
Hr	0.11 (0.01)	0.08–0.15	85.84 (15.60)	92.70 (9.94)
hH	0.34 (0.04)	0.26–0.44	110.49 (10.05)	377.88 (39.28)
Total forest floor	0.49 (0.04)	0.40–0.59	—	496.90 (42.46)
Site 3				
F	0.03 (0.002)	0.02–0.04	75.83 (3.98)	22.75 (2.40)
Hr	0.12 (0.03)	0.05–0.20	78.93 (4.94)	93.13 (21.38)
Hh	0.21 (0.05)	0.09–0.38	135.99 (9.96)	288.30 (73.91)
Total forest floor	0.41 (0.08)	0.19–0.70	—	404.19 (64.68)

Note: Values are means with SEs given in parentheses of three to five pits.

the forest floor and mineral soil horizons, although mean concentrations of SON, total N, and NH₄⁺ were highest in the mineral soil. There were significantly higher contents (g·m⁻²) of total N and SON in the Hh horizon than in the mineral soil, Hr, and F horizons, and SON contents were lowest in the F horizon. Nitrate and NH₄⁺ contents, however, did not differ among horizons. SON concentrations (g·m⁻³) differed significantly among sites, and there were significant site × horizon interactions for SON and NH₄⁺ concentrations and NO₃⁻ and NH₄⁺ contents.

Fine roots of the three species were not uniformly distributed down the profile, both in terms of density and biomass. Hemlock had significantly higher root densities in the upper forest floor horizons (F and Hr) than in the Hh and upper mineral soil, and salal had greater densities in the F and Hr than in the mineral soil (Table 3). Cedar fine root densities were not significantly different among horizons, but the highest mean concentrations were in the Hh horizon. The distributions of total fine root biomass also differed among species. Cedar had significantly larger masses of fine roots in the Hh than in the mineral soil and F horizons. Salal had larger root biomass in the Hr and Hh than in the mineral soil, and hemlock had significantly larger biomass in the Hr than in the other horizons. Salal fine root densities and cedar and salal fine root biomasses differed significantly among sites, but there were no site × horizon interactions.

The mean fine root biomasses of cedar, hemlock and salal in the entire profile were 817, 620, and 187 g·m⁻², respectively. The fine root biomasses of the three species were not summed by horizon and compared among species because of the comparatively low salal root masses. Salal roots are very thin and have a large surface area to volume ratio. Mass is, therefore, a poor indicator of the relative absorptive capacity of the three species and should only be compared within a species.

Spearman rank correlations indicated significant relationships among species and between fine root distributions and N concentrations in CH forest floor and mineral soil horizons. Salal fine root densities were negatively correlated

with total N ($r_s = -0.762$, $p = 0.004$) and SON ($r_s = -0.727$, $p = 0.007$) concentrations. Hemlock fine root densities and total root biomass were also negatively correlated with total N ($r_s = -0.706$, $p = 0.01$). There were no significant relationships between inorganic N (NO₃⁻ and NH₄⁺) concentrations and cedar, hemlock, and salal fine root distributions. Hemlock and salal root densities were positively correlated, and cedar total root biomass in each horizon was positively correlated to that of salal (Table 4).

Discussion

The fine root distributions of western redcedar, western hemlock, and salal were measured in the fall to determine if the three species have distinct vertical distribution patterns. Peaks in standing fine root biomass have been measured in spring (Herman 1977; Keyes and Grier 1981; Burton et al. 2000), summer (Gholz et al. 1986; Burton et al. 2000) and fall (Vogt et al. 1981). Vogt et al. (1981) found seasonal fluctuations in fine root distributions in a 180-year-old *Abies amabilis* (Dougl. ex Loud.) Dougl. ex Forbes stand, with greater amounts of fine roots in the forest floor than in the mineral A horizon during the autumn. At other times of the year, greater amounts of fine roots were found in the mineral soil. Cedar, hemlock, and salal fine root distributions in CH forests may also change during the year, but we did not evaluate seasonal variation. September was chosen as the sampling month, because it is at the end of the aboveground growth period and so would include the fine roots produced during the growing season.

Roots have been observed to concentrate at horizon interfaces (Strong and La Roi 1983a) and to decrease in abundance with depth. The full depths of the F and Hr horizons were collected, but only the top 15 cm of Hh was sampled. Therefore, the fine root densities and biomasses in the Hh horizon may have been overestimated. To account for this potential overestimation, root biomasses were re-calculated using the fine root densities from the mineral soils, if they were less than the measured Hh densities. It was assumed that the densities in the Hh horizon below 15 cm would not

be lower than those found in the mineral soil. It was found that the re-calculated estimates were similar to those determined by using the densities in the upper Hh horizon. Thus, the results presented herein represent the distributions of cedar, hemlock, and salal fine root biomass distributions in CH forests.

Estimates of the total fine root biomass of cedar (817 g·m⁻²), hemlock (620 g·m⁻²), and salal (187 g·m⁻²) in the profiles were within the range of values reported for similar systems. Vogt et al. (1981) measured 870–1770 g·m⁻² of conifer fine root biomass in a 180-year-old *A. amabilis* stand. In a Scots pine (*Pinus sylvestris* L.) stand, Persson (1983) found that two ericaceous shrubs, *Calluna vulgaris* (L.) Hull and *Vaccinium vitis-idaea* L., had 62 and 158 g·m⁻² of fine root biomass, respectively. Messier and Kimmins (1991) measured 498 g·m⁻² of salal (and some *Vaccinium* spp.) fine root biomass (to a 45 cm depth) on an 8-year-old regenerating CH site but hypothesized that in old-growth CH forests, salal fine root biomass declines to less than 200 g·m⁻², which agrees with our estimates.

Cedar, hemlock, and salal had 86, 93, and 96% of their fine root biomass located in the forest floors in CH forests, respectively, and this concentration of roots in the organic horizons was probably the result of both greater root densities in these horizons and forest floor thickness. Salal and hemlock fine root densities in the F and Hr were up to 10 times greater than root densities measured in the lower horizons, and the depths of CH forest floors are beyond the upper ranges reported for similar forest systems in Washington and Oregon (Little and Ohmann 1988). Studies of other forest systems have also reported that the majority of roots are located in the upper 15–40 cm of soils or forest floors (see Herman 1977; Strong and La Roi 1983a; Messier and Kimmins 1991; Messier and Mitchell 1994), and in a chronosequence of *A. amabilis* stands, Vogt et al. (1981) found a shift in fine root distribution from mineral to forest floor horizons with increased stand age and forest floor development. This shift of root production to the forest floor likely is a result of additional rooting volume that becomes available with the accumulation of detritus (Grier et al. 1981).

Cedar, hemlock, and salal in old-growth CH forests have different vertical fine root distribution patterns. Hemlock and salal roots were concentrated in the upper forest floor, while cedar roots were distributed more evenly among horizons. Similar trends were observed by Chang and Handley (2000), who found that salal and cedar mainly rooted in the F and H of old-growth CH forests, respectively. Ericoid and ectomycorrhizal roots have also been noted to concentrate in surface soil horizons in many systems (Persson 1983; see Read 1991).

Factors including nutrient availability, interspecific competition, and forest floor and soil moisture content are known to influence fine root distributions (Coutts and Philipson 1977; Herman 1977; Eissenstat and Caldwell 1988; see review Robinson 1994; Rytter and Hansson 1996; Xu et al. 1997; Bhatti et al. 1998; Hodge et al. 1999) and may be important in the spatial arrangement of cedar, hemlock, and salal fine roots in CH forests. Cedar–hemlock forests on northern Vancouver Island receive an average of 1700 mm of precipitation annually (Prescott and Weetman 1994). The gravimetric moisture contents of the forest floors

Table 2. Total N, soluble organic N, and extractable NO₃⁻ and NH₄⁺ in the forest floor and upper 10 cm of mineral soil in old-growth CH forests.

Horizon	Soluble organic N		Nitrate N		Ammonium N		Total N	
	By volume (g·m ⁻³)*,†	By area (g·m ⁻²)	By volume (g·m ⁻³)	By area (g·m ⁻²)†	By volume (g·m ⁻³)†	By area (g·m ⁻²)†	By volume (g·m ⁻³)	By area (g·m ⁻²)
F	14.06 (4.05)	0.44 (0.11) ^c	0.015 (0.010)	0.001 (0.000)	0.162 (0.015)	0.005 (0.0004)	707.92 (37.87)	22.61 (1.52)
Hr	11.76 (0.59)	1.38 (0.01) ^{bc}	0.021 (0.017)	0.003 (0.002)	0.207 (0.111)	0.026 (0.014)	755.61 (42.07)	88.42 (2.00)
Hh	16.17 (3.41)	4.73 (0.14) ^a	nd	nd	0.100 (0.039)	0.028 (0.006)	1125.59 (54.65)	348.48 (44.94)
Ae/B	18.59 (5.56)	1.86 (0.56) ^b	0.010 (0.010)	0.001 (0.001)	0.407 (0.191)	0.041 (0.019)	1519.57 (350.75)	151.96 (35.08)

Note: Values are means of three measurements with SEs given in parentheses and are expressed by volume (g·m⁻³) and area (g·m⁻²). Significant differences among the means within N form and unit of measurement are indicated by different letters ($p < 0.05$) based on analysis of variance (ANOVA). nd, NO₃⁻ was below the detection limit (0.010 ppm NO₃⁻-N).

*Significant differences among sites based on ANOVA.

†Significant site × horizon interactions based on Tukey test for non-additivity.

Table 3. Density ($\text{g}\cdot\text{m}^{-3}$) and biomass ($\text{g}\cdot\text{m}^{-2}$) of cedar, hemlock, and salal fine roots in the forest floor and upper 10 cm of mineral soil in old-growth CH forests.

Horizon	Cedar		Hemlock		Salal	
	($\text{g}\cdot\text{m}^{-3}$)	($\text{g}\cdot\text{m}^{-2}$)*	($\text{g}\cdot\text{m}^{-3}$)	($\text{g}\cdot\text{m}^{-2}$)	($\text{g}\cdot\text{m}^{-3}$)*	($\text{g}\cdot\text{m}^{-2}$)*
F	979 (187) <i>a</i>	32 (6) <i>c</i>	2889 (117) <i>a</i>	91 (2) <i>b</i>	580 (79) <i>a</i>	20 (3) <i>ab</i>
Hr	1348 (234) <i>a</i>	161 (30) <i>ab</i>	3328 (211) <i>a</i>	447 (21) <i>a</i>	375 (56) <i>b</i>	53 (10) <i>a</i>
Hh	1677 (102) <i>a</i>	509 (37) <i>a</i>	318 (83) <i>b</i>	37 (10) <i>b</i>	288 (52) <i>ab</i>	106 (23) <i>a</i>
Ae/B	1161 (57) <i>a</i>	116 (6) <i>b</i>	457 (97) <i>b</i>	46 (10) <i>b</i>	81 (14) <i>c</i>	8 (1) <i>b</i>

Note: Each value is the mean (standard error) of 12–15 root measurements. Within species and unit of measurement, means followed by the same letter do not differ significantly. Asterisks indicate significant differences among sites. No significant site \times horizon interactions were detected. The results are based on analysis of variance (ANOVA) ($p < 0.05$).

Table 4. Spearman rank correlations (r_s) of cedar, hemlock, and salal fine root abundances.

	Cedar	Hemlock	Salal
Cedar	—	-0.007	0.242
Hemlock	-0.013	—	0.344**
Salal	0.494***	0.201	—

Note: Values above the diagonal are fine root densities ($\text{g}\cdot\text{m}^{-3}$) and below the diagonal are fine root biomass ($\text{g}\cdot\text{m}^{-2}$). Asterisks indicate significant correlations ($n = 54$ – 57): **, $p < 0.01$; ***, $p < 0.001$.

measured in September were up to 84% (wet mass basis) and increased with depth. Thus, it is possible that periodic overabundance of water influences cedar, hemlock, and salal root distribution patterns in these forests. Western redcedar is flood tolerant and frequently grows in wet soils, while western hemlock is most frequently found in fresh to moist soils (Klinka and Worrall 1989). Therefore, the relatively even distribution of cedar fine roots throughout the profile and the concentration of hemlock roots in the surface horizons may reflect the different tolerances of the two species to soil moisture regimes.

Cedar, hemlock, and salal fine root distributions also may be influenced by interspecific root competition. Roots in close proximity can be forced to utilize the same resources (Grubb 1994) and may interact through the production and release of allelochemicals, which negatively influence the growth of the other plant (Schoener 1983). Experiments that segregate the roots of a plant from the root systems of surrounding vegetation have shown increases in plant growth (Cook and Ratcliff 1984; Christy 1986) and changes in fine root biomass and distributions (Abrazhko 1982) by the isolated individual. Several studies examining plants growing in mixed and monoculture states have also shown that rooting patterns are altered when more than one species grows in the same area (D'Antonio and Mahall 1991; Fredericksen and Zedaker 1995). Thus, the greater proportion of cedar fine roots in lower horizons may be a response to competitive pressures.

The distributions of cedar, hemlock, and salal roots in CH forests also may be influenced by nutrient availability. Under field and greenhouse conditions, fine roots tend to proliferate in areas with high nutrient concentrations (Coutts and Philipson 1977; Eissenstat and Caldwell 1988; see review Robinson 1994; Hodge et al. 1999), and several studies suggest the nutrient most limiting growth stimulates fine root production (Cuevas and Medina 1982; Friend et al. 1990). Nitrogen measurements in this study, however, suggest that N concentrations do not influence the distributions of cedar, hemlock, and salal fine roots in CH forest floor and mineral soil. Hemlock and salal root densities were negatively correlated with total N concentrations, and salal fine roots also showed a negative relationship with SON concentrations. Negative relationships between fine root distributions and N concentrations or net nitrification and mineralization rates have been found in other studies (Aber et al. 1985; Nadelhoffer et al. 1985), and it has been hypothesized that this inverse relationship is the result of rapid uptake of N in horizons with higher fine root densities (Bhatti et al. 1998). Instantaneous measurements of N concentrations, therefore, may estimate the amounts of N remaining following active absorption and poorly evaluate N availability.

Regardless of the factor responsible for the vertical distributions of cedar, hemlock, and salal fine roots, differences in the fine root distributions of the three species probably affect interspecific root interactions, competition for resources, and nutrient acquisition. The fine roots of salal and hemlock were concentrated in the upper forest floor and the fine root density distributions of the two species were correlated. These patterns indicate that salal and hemlock fine roots intermingle and have overlapping root depletion zones and, as such, probably have to share the resources in these horizons (Nye and Tinker 1977; Fredericksen and Zedaker 1995). Fraser et al. (1995) showed that hemlock growth was negatively influenced by the presence of salal, suggesting that the two species compete and that salal may be a strong competitor for N. Recent research has also indicated that both species can take up amino acids (Bennett et al., in preparation³) and have similar abilities to utilize a variety of organic and inorganic N compounds (Bennett and Prescott, in review⁴). Thus, hemlock and salal roots growing in the same forest

³J.N. Bennett, R.D.G. Guy, and C.E. Prescott. Amino acid uptake by western redcedar, western hemlock and salal in temperate cedar–hemlock forests on northern Vancouver Island. In preparation.

⁴J.N. Bennett and C.E. Prescott. Organic and inorganic nitrogen uptake by western redcedar, western hemlock and salal in mineral-N limited cedar–hemlock forests. Submitted to Ecology. In review.

floor horizons would be forced to share the same pool of available N. Nitrogen limits the growth of vegetation in CH forests. Therefore, salal and hemlock would compete for N.

In contrast to hemlock and salal, cedar fine roots were more evenly distributed in the CH forest floor and mineral soil horizons, and the cedar fine root densities were not significantly correlated with those of the other two species. However, the salal–cedar root density correlations were almost significant ($p = 0.07$), and both species had similar biomass allocation patterns indicated by the root biomass correlation. This significant relationship was largely a result of the large amounts of cedar and salal fine roots in the Hh horizons. Thus, there is some overlap between cedar and salal fine root distributions, but the degree of fine root overlap between cedar and salal is less than that of salal and hemlock. This is consistent with the findings of Fraser et al. (1995), in that the growth of cedar was not affected by salal vigour. Cedar probably does not experience the same degree of competition, and by having more fine roots in the lower organic and mineral soil horizons, it is able to access resources, including N, that are less exploited by salal and hemlock. Other studies have also found spatial separation of fine rooting systems in mixed-species stands (Mikola et al. 1966; McQueen 1968; Persson 1983; Strong and La Roi 1983b; Gholz et al. 1986; Jonsson et al. 1988; Fredericksen and Zedaker 1995; Mou et al. 1995) and deserts (Yeaton et al. 1977; Manning and Barbour 1988), and several of these showed that plants with spatially separated fine roots had higher productivity levels (Yeaton et al. 1977; Manning and Barbour 1988; Fredericksen and Zedaker 1995). The same phenomena may occur in cedar in CH forests, and the spatial arrangement of fine roots may contribute to the better growth of cedar than hemlock in these forests.

In conclusion, cedar, hemlock, and salal have different distributions of fine roots in CH forest floor and upper mineral soil horizons. Salal and hemlock roots were mostly in the upper forest floor, so these species interact and compete more for the same pool of N. Cedar roots were evenly distributed, which would allow them to access N pools used less by the other species. These differences in fine root distribution patterns may facilitate the co-occurrence and different productivities of the three species in N-limited CH forests.

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