Fine-root decomposition and N dynamics in coniferous forests of the Pacific Northwest, U.S.A.

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Abstract: We examined the effects of species, initial substrate quality, and site differences (including temperature, precipitation, and soil N availability) on fine-root (<2 mm diameter) decomposition in litter bags and its N dynamics in Sitka spruce (*Picea sitchensis* (Bong) Carrière), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) forests in Oregon, U.S.A. Species significantly influenced fine-root mass loss during the first 2 years of decomposition. Over the same period, site differences had little impact on decomposition of fine roots. The percentage of initial mass remaining of decomposing fine roots fitted a single-exponential model. The decomposition rate constant (k) for all 15 species examined ranged from 0.172 year^{-1} for Engelmann spruce (*Picea engelmanni* Parry ex Engelm.) to 0.386 year^{-1} for Oregon ash (*Fraxinus latifolia* Benth.). Initial C quality indices (e.g., cellulose concentration, lignin concentration) of fine roots were correlated with fine-root decomposition rates. In contrast, initial N concentration and soil N availability were not correlated with fine-root decomposition rates. The rate of N released from decomposing roots was positively correlated with the initial N concentration of the fine roots. The data suggest that decomposing fine roots could release at least 20 kg N/ha annually in mature Douglas-fir forests of the Pacific Northwest.

Résumé : Nous avons étudié les effets dus à l'espèce, à la qualité initiale du substrat et aux différences entre les sites (incluant la température, la précipitation et la disponibilité de N dans le sol) sur la décomposition des racines fines (<2 mm de diamètre) en sacs de litière et la dynamique de N dans des forêts d'épinette de Sitka (*Picea sitchensis* (Bong.) Carrière), de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) et de pin ponderosa (*Pinus ponderosa* Dougl. ex P. & C. Laws.) en Oregon, aux États-Unis. L'espèce influence significativement la perte de masse des racines fines pendant les deux premières années de décomposition. Pendant la même période, les différences entre les sites ont eu peu d'impact sur la décomposition des racines fines. Ce qui restait de la masse initiale suite à la décomposition des racines fines suit une courbe exponentielle unique. La constante du taux de décomposition (k) pour l'ensemble des 15 espèces étudiées varie de 0,172 an^{-1} pour l'épinette d'Engelmann (*Picea engelmannii* Parry ex Engelm.) à 0,386 an^{-1} pour le frêne de l'Oregon (*Fraxinus latifolia* Benth.). Les indices de qualité du C initial (p. ex., concentration de cellulose et de lignine) des racines fines sont corrélés aux taux de décomposition des racines fines. Au contraire, la concentration initiale de N et la disponibilité de N dans le sol ne sont pas corrélées aux taux de décomposition des racines fines. Le taux de libération de N provenant de la décomposition des racines fines est positivement corrélé à la concentration initiale de N dans les racines fines. Les données indiquent que la décomposition des racines fines pourrait libérer au moins 20 kg N/ha annuellement dans les forêts matures de douglas de Menzies dans la région du Pacifique Nord-Ouest.

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Introduction

Fine roots are important structural and functional components of forested ecosystems (Persson 1980; Grier et al. 1981; Santantonio and Hermann 1985). A large proportion of forest production is allocated to fine roots, resulting in a large flux of C and nutrients into the belowground system (Vogt et al. 1986; Kurz et al. 1996; Cairns et al. 1997). Although tree root systems store large amounts of organic matter and nutrients in forest ecosystems, information on the rates and controls of fine-root decomposition is scant, especially compared with the wealth of data on aboveground litter decomposition (Gosz et al. 1973; Fogel and Cromack 1977; Melillo et al. 1982; Berg and Ekbohm 1983; Harmon et al. 1990). To better understand the nutrient cycling, soil organic matter dynamics, and C stores of forest ecosystems, more fine-root decomposition studies are needed.

Past studies on root dynamics have primarily focused on production and growth (Persson 1980; Grier et al. 1981; McClaugherty and Aber 1982; Hendrick and Pregitzer 1992; Steele et al. 1997; Lehmann and Zech 1998). The few root decomposition studies that have been conducted were either short-term (i.e., usually 1 year) (Camiré et al. 1991; Conn and Day 1997) or observational studies using a chronosequence approach (Yavitt and Fahey 1982; Chen et al. 2001). Experimental studies testing factors influencing root decomposition directly are even fewer in number (Fahey et al. 1988; King et al. 1997; Ostertag and Hobbie 1999), but they are critical to developing a predictive understanding of root decomposition (Camiré et al. 1991; Chen 1999).

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Although the factors affecting root decomposition are generally known, the relative importance of biotic and abiotic factors and how they interact is poorly understood. The major biotic factors that may affect root decomposition include the concentration of N and lignin in roots as well as the decay organisms present in the soil and their colonization patterns (Berg 1984; Parker et al. 1984; Camiré et al. 1991; Scheu and Schauermann 1994; Hobbie 1996; Chen et al. 2001). So far, the initial lignin/N concentration ratio seems to be the best biotic predictor of root decomposition (Berg 1984; McClaugherty et al. 1984; Aber et al. 1990; Camiré et al. 1991; Hobbie 1996). Abiotic factors with the potential to influence root decomposition include temperature, moisture, oxygen concentration, and soil properties such as texture and N availability. Of these, temperature and moisture content are regarded as the main abiotic factors influencing root decomposition (Vogt et al. 1986; Hobbie 1996; King et al. 1997; Chen et al. 2000).

Starting in June 1995, we used litter-bag techniques to measure the effects of root species and size on long-term root decomposition at three locations in the Pacific Northwest, U.S.A.: Cascade Head Experimental Forest, H.J. Andrews Experimental Forest, and Pringle Falls Experimental Forest. This paper presents the analysis of the first 2 years of fine-root decomposition data from the 10-year experiment. Four questions that are important to the forests of the Pacific Northwest were addressed: (1) how did the decomposition of fine roots vary with species, (2) could the decomposition rate constants of fine roots be predicted from the initial substrate quality indices, (3) how did the decomposition of fine roots vary under different climatic conditions, and (4) how did the N content change during fine-root decomposition?

Study sites

This decomposition time series study was conducted in Sitka spruce (*Picea sitchensis* (Bong) Carrière), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) dominated forests at Cascade Head (CAH), H.J. Andrews (HJA), and Pringle Falls (PRF) experimental forests in Oregon, respectively. These three sites form a climatic gradient from warm and wet at CAH to cool and dry at PRF.

CAH is located on the Pacific coast near the town Otis, Oregon. The climate is maritime, with a mean annual temperature of 10°C and mean annual precipitation of 3420 mm. The soils are silt loams to silty clay loams derived from marine siltstones, moderately well drained, and have a high content of organic matter and N. The dominant forest type is a mixture of western hemlock (*Tsuga heterophylla* (Raf.) Sarg) and Sitka spruce, although small stands dominated by Douglas-fir also occur. HJA is located 80 km east of the city Eugene, Oregon, on the west slope of the Cascade Range. The climate is also maritime, with wet, relatively mild winters and dry, cool summers. Mean annual temperature is 8.5°C and mean annual precipitation is 2300 mm. Soils are deep, well-drained Dystrochrepts; slope gradient ranges from 20 to 60%. The forests are dominated by Douglas-fir and western hemlock at low elevation (1050–1550 m) (Franklin and Dyrness 1973). PRF is located 57 km southwest of the city Bend, Oregon, east of the Cascades. The climate is modified continental, with a mean annual temperature of 5.7°C and mean annual precipitation of 525 mm. Soils are coarse loamy sand derived from aerially deposited dacite pumice. Topography is rolling to gentle slopes, and the elevation ranges from 1310 to 2470 m. The forests are dominated by ponderosa pine and lodgepole pine (*Pinus contorta* Dougl. ex Loud.).

Materials and methods

Experimental design

The overall experimental design for the root decomposition time series was a split-split plot with three sites (CAH, HJA, PRF), four plots within each site, and 15 species (Tables 1 and 2). Of the 15 species examined, red alder (*Alnus rubra* Bong.), Douglas-fir, western hemlock, and ponderosa pine occurred at every site and harvest time and hence were named "backbone" species. At each site, four plots that were representative of the area's forest composition were selected (Table 1). The plots were close to each other (the maximum distance between plots was about 10 km) and they had similar soil types.

Root preparation and placement

Of the 15 species examined, 11 were coniferous and 4 were deciduous. All the species are common in the Pacific Northwest. Fine roots of these species were obtained from Bend Pine, H.J. Stone, and Wind River nurseries in Oregon and Washington in the early spring of 1994. The fine roots (<2 mm diameter) were trimmed from the nursery seedlings, and they were then transported to Corvallis, Oregon, where they were cleaned by rinsing with tap water, spread on trays, and air-dried at room temperature to a constant mass. The air-dry moisture contents of fine roots ranged from 6.0 to 9.5% across all species, but the standard deviation within each species was <0.5%, as determined by 8 or 10 samples. Approximately 10 g of air-dried fine roots were weighed and placed in 20 × 20 cm dacron cloth litter bags with an effective mesh size of 50 μm. Each litter bag was tagged with a unique numbered aluminum tag. Subsamples were retained for initial moisture, ash, and chemical analyses.

Root samples that were to be harvested at a given time were tethered together by a nylon line. Tethered root samples were then buried in the soil at a depth of 20 cm at each plot in the three sites in June 1995. A total of 1933 fine-root bags were buried at the 12 plots for a 10-year study.

Determination of mass loss

Mass loss of fine roots was estimated from changes in ash-free dry mass of roots based on samples harvested at different time intervals (Table 2). The fine roots of backbone species were harvested seven times during the 2.5 years of decomposition, and those of "non-backbone" species were harvested two or three times in the same period. During harvesting, each root litter bag was placed in a ziplog plastic bag on site to prevent moisture loss after its retrieval from the soil. Fine-root samples were then returned to the Corvallis laboratory, carefully brushed free of soil and other debris, and ingrowing roots were removed. Samples were dried to a constant mass at 65°C and weighed. Dried root samples were ground in a Wiley mill and passed through a

Table 1. Climate and tree species for the plots used for root decomposition.

Site	Tree species	Plot No.	Elevation (m)	Mean annual air temp. (°C)[a]	Mean annual soil temp. (20-cm depth) (°C)[a]	Mean annual precipitation (mm)
Cascade Head	*Tsuga heterophylla*, *Picea sitchensis*	1	233	8.70	9.94	3420
		2	400	8.49	9.16	3420
		3	266	8.63	9.86	3420
		4	200	8.96	10.01	3420
H.J. Andrews	*Tsuga heterophylla*, *Pseudotsuga menziesii*	1	1065	6.91	6.96	2290
		2	935	7.51	7.61	2070
		3	535	7.88	7.97	2090
		4	865	7.68	7.75	2190
Pringle Falls	*Pinus ponderosa*, *Pinus contorta*	1	1400	6.03	6.87	525
		2	1533	5.98	6.80	525
		3	1766	4.66	5.17	525
		4	1800	4.28	4.73	525

[a]Based on data from December 1995 to March 1998.

Table 2. Harvesting history of fine-root (<2 mm diameter) samples at the three study sites.

Scientific name	Common name	Incubation period (months)						
		3	6	9	12	18	24	30
Pinus ponderosa Dougl. ex P. & C. Laws.*	Ponderosa pine	x	x	x	x	x	x	x
Pseudotsuga menziesii (Mirb.) Franco*	Douglas-fir	x	x	x	x	x	x	x
Tsuga heterophylla (Raf.) Sarg*	Western hemlock	x	x	x	x	x	x	x
Alnus rubra Bong.*	Red alder	x	x	x	x		x	
Acer macrophyllum Pursh	Bigleaf maple		x		x		x	
Abies magnifica A. Murr.	California red fir		x		x		x	
Calocedrus decurrens Torr.	Incense-cedar		x		x		x	
Fraxinus latifolia Benth.	Oregon ash		x		x		x	
Picea engelmanni Parry ex Engelm.	Engelmann spruce		x		x		x	
Pinus contorta Dougl. ex Loud.	Lodgepole pine		x		x		x	
Pinus monophylla Torr. & Frem.	Nut pine		x		x		x	
Thuja plicata Donn ex D. Don	Western redcedar		x		x		x	
Abies concolor Lindl. ex Hildebr.	White fir				x		x	
Abies procera Rehd.	Noble fir				x		x	
Acer rubrum L.	Red maple				x		x	

Note: Asterisks indicate the backbone species. An "x" indicates that the incubating root samples were harvested.

fine screen (1 mm). Samples were stored in 20-mL vials to prevent moisture changes prior to analyses for ash and N concentration.

Wet chemistry analyses

All 936 harvested root samples were analyzed for ash and N concentration, and fresh fine roots of the 15 species were also analyzed for organic constituents. The decomposed root samples were scanned by near infrared reflectance spectroscopy (NIRS) with a NIRSystems 6500 analyzer (NIRSystems Inc., Silver Spring, Md., U.S.A.) to predict ash and N concentrations (Chen 1999). The NIRS calibration for ash and N was conducted on the samples obtained from the three sites, using the ash and N concentrations of fine roots obtained from wet chemistry analyses. The NIRS predictions were validated against samples that had not been used as part of the calibration process. The details of the calibration, validation, and prediction are described in Chen (1999). All the mass and N data reported in this paper were ash-free values.

We analyzed ash and N concentrations of the selected root samples. The ash concentration of 280 root samples was determined by heating in a muffle furnace at 500°C for 4 h. In addition, the C and N concentrations of 160 root samples were measured by a Carlo Erba C/N analyzer.

The initial organic constituents of fresh fine roots examined in the time-series study were analyzed by proximate analysis. The constituents analyzed included nonpolar extractives (fats, oils, and waxes), using dichloromethane as the extratant (TAPPI 1975), hot water soluble phenols (Folin–Denis method, Allen 1989), hot water soluble simple sugars (phenol-sulfuric acid assay, DuBois et al. 1956), acid-hydrolyzable fraction (cellulose, hemicellulose, and starch, hydrolysis followed by the phenol-sulfuric acid assay, DuBois et al. 1956), and acid-resistant fraction (Effland 1977). Although the acid-resistant fraction includes other recalcitrant C fractions besides lignin (e.g., suberin), we will simply refer to it as "lignin". In addition, the initial ash, C, and N concentrations of fine roots were measured. One stan-

dard pine needle sample with known initial substrate quality and N concentration was included in each batch to assure quality control.

Soil N availability

The soil N availability of the three sites was measured by ion-exchange resin bags (Binkley and Matson 1983). Resin bags were prepared by placing mixed-bed ion-exchange resin (J.T. Baker Chemical, catalog No. 4631-1) in nylon stockings. Each bag contained 30 g moist mass of resin (equivalent to about 16.5 g dry mass) with anion- and cation-exchange capacities of 2.6 mequiv./g. In June 1995, in each of the plots where roots had been placed, we buried 10 resin bags connected by a nylon line at a depth of 20 cm in the soil. These resin bags were collected 1 year later and air dried. Four to five grams of dry resin of each resin sample were extracted with 50 mL of 1 M KCl. Ammonium and nitrate concentrations, as measurements of soil N availability, were determined by colorimetric analysis on an Alpkem autoanalyzer (Alpkem, Wilsonville, Oreg., U.S.A.).

Microclimate

Temperature data were collected at each plot starting from December 1995. We measured the soil temperature (20-cm depth) as well as air temperature (1-m height) using thermistors (YSI 44006, YSI Inc., Yellow Springs, Ohio). Air and soil temperatures were recorded hourly and every 12 h, respectively. The moisture content of root samples was calculated as the water mass of the root sample divided by oven-dry mass of the root sample after each harvest.

Statistical analysis

Analysis of variance with a split-split-plot experimental design was used to test the effects of site, species, and their interaction on fine-root decomposition using the first- and second-year data.

A single-exponential model was fitted to the remaining mass of fine roots using the least square method of the GLM procedure of SAS (SAS Institute Inc. 1998):

$$Y_t = Y_0 \, e^{-kt}$$

where Y_0 is the percentage of initial mass of fine roots, Y_t is the percentage of initial mass remaining at time t, and k is the decomposition rate constant. The k value was calculated from the linear regressions of the percentage of initial mass remaining, transformed into natural logarithms (ln), versus time. For each species, the mean percentage of initial mass remaining of four plots at each site rather than initial mass remaining of individual litter bags was used in these regressions. The slope of these regressions was k. The half-life of each species was calculated from these regressions.

The effects of initial root substrate quality on k of fine roots were evaluated by the P value of a simple regression. A linear regression was developed with k as the dependent variable and each initial root quality index as the independent variables. Finally, multiple linear regressions using a stepwise procedure were applied to determine the best predictive model of k of fine roots. Indices of initial root quality in these analyses included the initial concentrations of all the organic fractions as well as C, N, C/N ratio, and lignin/N ratio. Analysis of variance was used to test the effects of site on soil N availability.

All statistical tests were performed with the GLM procedure of SAS (SAS Institute Inc. 1998). Statistical tests were judged significant if $0.05 > P > 0.01$ and highly significant if $P \leq 0.01$.

Results

Fine-root decomposition and mass loss

The split-split-plot analysis of variance showed that fine-root decomposition in the 4 backbone species and 11 non-backbone species did not significantly differ among the three study sites ($P > 0.05$) (Table 3). In contrast, species appeared to significantly ($P < 0.05$) influence the decomposition of fine roots during the first 2 years of decomposition, although exceptions occurred in the non-backbone species (Table 3). The interaction of species and site was not significant at any time for either backbone species or non-backbone species (Table 3).

Fine roots showed a rapid loss of mass during the first few months, followed by a dramatic slowing of the decomposition rate (Fig. 1). Red alder lost 31.7 to 36.8% of its initial mass in the first 3 months, while Douglas-fir, western hemlock, and ponderosa pine lost one-fourth of their mass over the same time period. During the 2 years of decomposition, red alder lost about 55% of its initial mass. The mass loss curves of Douglas-fir, western hemlock, and ponderosa pine were very similar to each other, with all three species losing about 40% of their initial mass after 2 years (Fig. 1A). Similar temporal patterns were observed in the fine-root decomposition of the other 11 species (Figs. 1B and 1C). Of the 11 examined species, Oregon ash had the fastest decomposition, losing 43.4% of initial mass, on average, at the three sites in the first 6 months; while incense-cedar (*Calocedrus decurrens* (Torr.) Florin), with the slowest decomposition in our study, only lost 16.8% during the same period. At the end of 2 years of decomposition, Oregon ash still decomposed the fastest, losing 63.2% of its initial mass, whereas incense-cedar continued to have the slowest decomposition, losing only 36.3% of its initial mass (Fig. 1).

Decomposition rate constant

A single-exponential model fit the remaining mass of decomposing fine roots. For all 15 species, the model was highly significant ($P \leq 0.01$). The determination coefficients (R^2) of the regressions for these species were from 0.61 to 0.92. The decomposition rate constant (k) of fine roots varied by species (Table 4). The k for all 15 species ranged from 0.172 to 0.386 year^{-1}. The order of increasing k among the 15 species was as follows: Engelmann spruce < nut pine (*Pinus monophylla* Torr. & Frem.) < Douglas-fir < incense-cedar < western hemlock < lodgepole pine < ponderosa pine < bigleaf maple < western redcedar < red alder < red maple < noble fir < California red fir < white fir < Oregon ash (Table 4). The half-life of Oregon ash was 1.7 years. In contrast, the species with the slowest decomposition, Engelmann spruce, had a half-life of 3.9 years. All the Y intercepts of the linear ln-transformed regression were less than 100%, ranging from 76.1% (bigleaf maple) to 94.5%

Table 3. Results of the split-split-plot ANOVA for percentage of initial mass of fine roots remaining after the first and second years of field incubation at the three study sites.

	Decay age (years)	Source	Error term	*F*	df	*P*
Backbone species	1	S	R(S)	0.05	2, 47	0.95
		Sp*	Sp × R(S)	4.83	3, 47	0.03
		Sp × S	Sp × R(S)	0.71	6, 47	0.65
	2	S	R(S)	0.87	2, 47	0.50
		Sp*	Sp × R(S)	3.90	3, 47	0.05
		Sp × S	Sp × R(S)	1.10	6, 47	0.43
Non-backbone species	1	S	R(S)	0.1	2, 131	0.90
		Sp*	Sp × R(S)	5.9	10, 131	0.00
		Sp × S	Sp × R(S)	1.0	20, 131	0.50
	2	S	R(S)	0.7	2, 125	0.57
		Sp	Sp × R(S)	1.3	10, 125	0.28
		Sp × S	Sp × R(S)	0.9	20, 125	0.63

Note: Sp, species; S, site; R, repetition (i.e., plots within each site). Asterisks indicate statistically significant sources of variation ($P \leq 0.05$).

(incense-cedar), indicating an initial rapid period of mass loss (Harmon et al. 1999).

Controls of fine-root decomposition

Initial substrate quality

Initial substrate quality indices varied with species (Table 5). The mean fine-root N concentration of the 15 species was 1.4%, ranging from 0.9 to 2.2%. The concentration of water-soluble (WS) extractives in the fine-roots of these species averaged 23.4%, ranging from 16.5 to 31.7%. For the lignin concentration, the species mean was 22.9%. In general, roots of deciduous trees had higher N and water-soluble extractive concentrations and lower lignin concentrations than those of coniferous trees. For example, the N concentration of fine roots of the four deciduous trees averaged 1.7%, ranging from 1.2 to 2.2%, whereas N concentration averaged 1.3% in coniferous fine roots, ranging from 0.9 to 1.7%.

The decomposition rate constants of fine roots were significantly and negatively correlated with 7 of the 17 initial substrate quality indices (Table 6). These seven indices included total C concentration, lignin concentration, lignin + WS phenols, (lignin + WS phenols)/N, lignin/N, (lignin + cellulose)/N, and lignin–cellulose index. The correlation coefficients of these regressions ranged from 0.52 to 0.71. Cellulose concentration was the only initial substrate quality index significantly and positively correlated with the *k* value of fine roots. In contrast, the initial N concentration of fine roots showed a poor correlation with *k* (Table 6). Multiple-regression analysis indicated that the best model for predicting the *k* value of fine roots using the initial substrate quality index was

$$k = 0.365 - 0.012[(\text{lignin} + \text{WS phenols})/\text{N}]$$

The model was highly significant ($P \leq 0.01$) with a determination coefficient (R^2) of 0.66.

Soil N availability

The results of the ion-exchange resin bags indicated that there were significant differences in soil N availability (as estimated by soil ammonium availability and the total availability of soil ammonium and soil nitrate) among the three sites (Table 7). Soil ammonium availability of CAH was 99 μg/g air-dry resin, the highest among the three sites. HJA and PRF had very similar soil ammonium availability, although no clear difference of soil nitrate availability index occurred among three sites ($P = 0.30$).

Soil temperature and root moisture dynamics

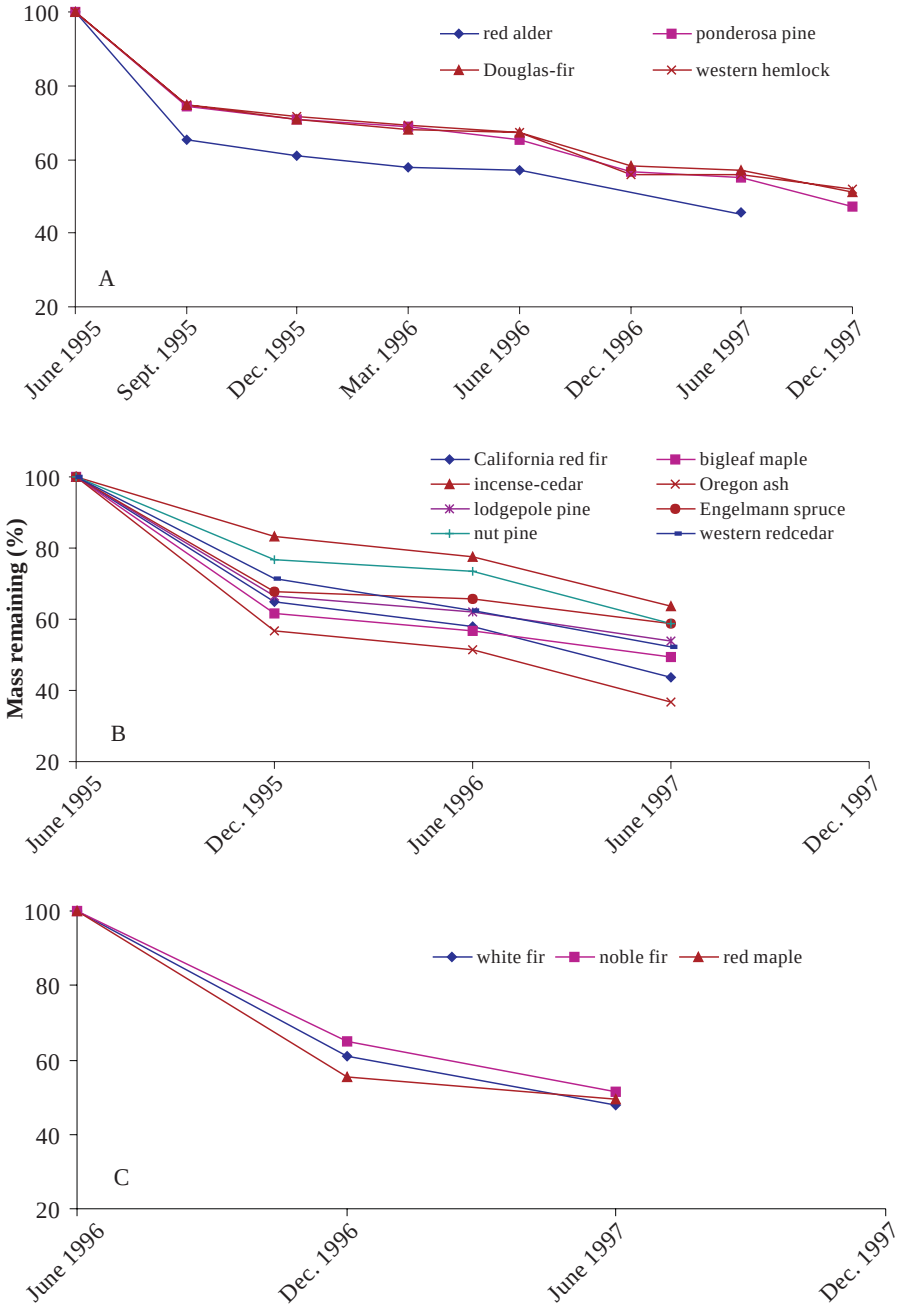
Soil temperature and root moisture varied among the sites (Figs. 2–3). Yearly fluctuations in monthly mean soil temperature at 20-cm depth varied from 6.6 to 13.4°C, 1.8 to 14.9°C, and 0.9 to 14.8°C at CAH, HJA, and PRF, respectively (Fig. 2). Soil temperature at PRF could reach as low as 1°C in winter and early spring, while the lowest soil temperature at HJA was around 2°C in December (Fig. 2). The soil temperature at CAH is much milder in comparison with the HJA and PRF sites. The moisture content of dead fine roots at CAH usually ranged from 300 to 400% (Fig. 3). In contrast, fine-root moisture content at PRF generally ranged from 100 to 200%. At HJA, fine-root moisture content was intermediate and averaged 200 to 300%.

Nitrogen dynamics

The N content of the fine roots of the four backbone species exhibited a quick decrease in first 3 months and then showed either a consistent declining trend over time or a short phase of N accumulation. For these four species, however, more N was released than accumulated in first 2 years of fine-root decomposition (Fig. 4 and Table 8). This pattern was observed at all three sites, and site had no significant effect on the pattern (Fig. 4). Red alder and Douglas-fir experienced a consistent N release during the first 2 years of decomposition at all three sites. However, ponderosa pine and western hemlock accumulated some N after the initial rapid release of N.

Similarly, N was released from all 11 non-backbone species during the first 2 years of decomposition (Table 8). After 1 year of decomposition, the decomposing fine roots released 8.7% (incense-cedar) to 53.3% (red maple) of their

Fig. 1. Fine-root decomposition in Oregon. (A) Fine roots of backbone species; (B) fine roots of non-backbone species that were harvested three times in the first 2 years of decomposition; and (C) fine roots of non-backbone species that were harvested twice in the first 2 years of decomposition.



initial N content. Incense-cedar and red maple continued to be the slowest and fastest species, releasing 26.1 and 63.1% of initial N content of fine roots, respectively, after 2 years of decomposition.

The initial N concentration of fine roots was positively correlated with the rate of N release and accounted for 80% of the variation in the rate of N release (Fig. 5). Of the 15 species, red maple had the highest initial N concentration, 2.2% of dry mass, and released up to 63% of its initial N content in 2 years of decomposition. Given the initial N concentration of the 15 species (mean 1.4%), the decomposing fine roots released, on average, approximately 29% of their original N content in 2 years (Fig. 5).

Discussion

Controls of fine-root decomposition

Biotic factors and initial substrate quality

For fine-root decomposition, all the Y_0 intercepts in the single-exponential model were much less than 100% (Table 4), suggesting a rapid loss of mass initially, followed by a period of slower loss (Harmon et al. 1990, 1999). While our sampling interval was less than optimal for using a double-exponential model to determine the exact decomposition rate of the earlier stage, it still indicates that the process of fine-root decomposition is composed of an earlier stage of rapid

Table 4. Regressions coefficients of the single-exponential model used to estimate the decomposition rate constant (k) of fine roots in the Pacific Northwest, U.S.A.

	Regression coefficients[a]				
Species	Y_0 (%)	k (year^{-1})[b]	R^2[c]	N[d]	Half-life (years)
Oregon ash	76.8	0.386 (0.057)	0.85**	10	1.7
White fir	91.0	0.339 (0.059)	0.87**	7	2.0
California red fir	82.5	0.331 (0.049)	0.85**	10	2.0
Noble fir	93.1	0.313 (0.068)	0.81**	7	2.1
Red maple	84.0	0.295 (0.074)	0.76**	7	2.3
Red alder	73.4	0.260 (0.043)	0.72**	16	2.6
Western redcedar	84.6	0.257 (0.040)	0.83**	10	2.6
Bigleaf maple	76.1	0.242 (0.058)	0.68**	10	2.8
Ponderosa pine	81.7	0.220 (0.028)	0.79**	22	3.0
Lodgepole pine	80.0	0.217 (0.049)	0.71**	10	3.1
Western hemlock	82.3	0.217 (0.025)	0.82**	22	3.1
Incense-cedar	94.5	0.201 (0.021)	0.92**	10	3.3
Douglas-fir	81.2	0.197 (0.028)	0.75**	22	3.4
Nut pine	89.0	0.187 (0.037)	0.76**	10	3.6
Engelmann spruce	79.9	0.172 (0.049)	0.61**	10	3.9

[a]The regression was of the form $Y_t = Y_0\ e^{-kt}$, where Y_t is the percentage of initial mass remaining at time t (years), Y_0 is the percentage of initial mass, and k is the the decomposition rate constant of the fine roots.
[b]The values in parentheses are standard errors.
[c]**, $P < 0.01$.
[d]Each data point is the mean of four samples at each site.

Table 5. Chemical characteristics of fresh fine roots (% of dry mass).

Species	N	C	NPE	WS extractives	WS sugar	WS phenols	AHF cellulose	ARF lignin
Bigleaf maple	1.5	45.8	5.2	20.0	4.2	2.1	52.5	22.4
California red fir	1.6	45.9	7.2	27.4	6.0	2.9	43.8	21.6
Douglas-fir	1.3	47.0	6.3	21.9	5.3	5.3	42.2	29.6
Engelmann spruce	1.2	46.7	7.8	22.0	6.4	3.0	43.6	26.5
Incense-cedar	1.0	48.0	15.2	16.5	3.5	4.2	42.8	25.5
Lodgepole pine	1.7	46.2	3.8	25.0	5.5	2.0	44.9	26.2
Noble fir	1.7	44.7	7.8	23.2	5.0	2.9	47.0	22.0
Nut pine	0.9	46.3	16.1	16.9	4.3	2.1	41.3	25.6
Oregon ash	1.2	46.0	5.8	28.7	7.5	2.2	49.6	15.9
Ponderosa pine	1.0	47.3	11.7	21.2	4.9	2.3	43.8	23.3
Red alder	1.8	45.1	7.3	31.7	6.8	7.5	45.9	15.1
Red maple	2.2	46.3	4.1	24.0	5.8	2.9	46.4	25.5
Western hemlock	0.9	45.2	7.5	28.0	6.6	6.2	42.9	21.6
Western redcedar	1.6	46.3	11.8	22.6	3.6	4.0	45.1	20.5
White fir	1.6	45.1	6.0	21.3	3.0	3.5	50.0	22.7
Mean	1.4	46.1	8.2	23.4	5.2	3.5	45.5	22.9
SE	0.4	0.9	3.8	4.3	1.3	1.6	3.2	3.9

Note: All values are expressed on an ash-free dry mass basis. NPE, nonpolar extractives (fats, oils, and waxes); WS extractives, water-soluble extractives; WS sugar, water-soluble carbohydrate; WS phenols, water-soluble phenols, expressed as percent tannic acid equivalents; AHF cellulose, acid-hydrolyzable fraction, including cellulose and hemicellulose; ARF lignin, acid-resistant fraction, including other recalcitrant C fractions besides lignin (e.g., suberin), though simply referred to as lignin here. The summation of NPE, WS extractives, AHF cellulose, and ARF lignin is equal to 100%. SE, standard error.

mass loss and a later stage of slow mass loss (Fig. 1). The mass loss in the earlier stage was largely associated with labile C, such as initial water-soluble (WS) extractives of fine roots, while the mass loss in the later stage was probably correlated with recalcitrant C, such as lignin concentration (Chen 1999). It is important to be aware that the k values from the single-exponential model may be misinterpreted unless the Y_0 intercept is also examined. Since the Y_0 intercepts are much lower than 100%, the mass loss of fine roots will be grossly underestimated with the single-exponential

Table 6. Effects of initial substrate index on decomposition rate constants (*k*) of fine roots.

Initial substrate index	*F*	df	*P*	*r*
C*	4.81	1, 14	0.05	–0.52
N	3.47	1, 14	0.09	0.46
C/N	4.42	1, 14	0.06	–0.50
NPE	2.82	1, 14	0.12	–0.42
WS extractives	3.65	1, 14	0.08	0.47
WS sugar	0.38	1, 14	0.55	0.17
WS phenols	0.37	1, 14	0.55	–0.17
WS phenols/N	2.13	1, 14	0.17	–0.37
Cellulose*	8.39	1, 14	0.01	0.62
Lignin*	7.81	1, 14	0.02	–0.61
Lignin + WS phenols*	12.75	1, 14	0.00	–0.71
(Lignin + WS phenols)/N*	13.33	1, 14	0.00	–0.71
Lignin/N*	12.49	1, 14	0.00	–0.70
Cellulose/N	1.86	1, 14	0.20	–0.35
(Lignin + cellulose)/N*	5.24	1, 14	0.04	–0.54
LCI ratio*	8.78	1, 14	0.01	–0.63
Lignin/WS phenols	0.61	1, 14	0.45	–0.21

Note: Asterisks indicate statistically significant sources of variation in the correlation between *k* and substrate quality index ($P \leq 0.05$). NPE, nonpolar extractives (fats, oils, and waxes); WS extractives, water-soluble extractives; WS sugar, water-soluble carbohydrate; WS phenols, water-soluble phenols, expressed as percent tannic acid equivalents; cellulose, acid-hydrolyzable fraction, including cellulose and hemicellulose; lignin, acid-resistant fraction, including other recalcitrant C fractions besides lignin (e.g., suberin), though simply referred to as lignin here; LCI ratio, lignin/(cellulose + lignin), where cellulose refers to acid-soluble cellulose. Cellulose in (lignin + cellulose)/N refers to acid-soluble cellulose. Phenols in lignin + phenols, (lignin + phenols)/N, and lignin/phenols refer to water-soluble phenols.

model if only the *k* value and the 100% Y_0 intercept are used in the model.

Our results suggest that the controls of fine-root decomposition were closely associated with initial C quality (e.g., lignin) instead of the initial N concentration of fine roots or soil N availability (Table 6). Of the initial C quality indices, lignin concentration significantly showed the negative impact on *k* of fine roots. Other initial C quality indices such as WS extractives and WS sugar concentration had poor correlations with the *k* value of fine roots. Similarly, both the initial N concentration of fine roots and soil N availability showed no significant correlation with the *k* values of fine roots, although soil N availability varied significantly among sites. In the Pacific Northwest coniferous forests, N strongly limits net primary production (Franklin and Dyrness 1973; Sollins et al. 1980), but it does not appear to limit the decomposition of fine roots. Control of root decomposition by initial C quality, such as lignin concentration, instead of N concentration is in agreement with a number of other root decomposition studies (Hobbie 1996, 2000; Conn and Day 1997). Hobbie (1996) indicated that the decomposition of plant litter in Alaskan tundra was related more to lignin and acid-soluble carbohydrates than to the relative availability of N. Conn and Day (1997) reported that increasing soil N availability had no effect on the rate of *Spartina patens* root decomposition.

Table 7. Soil nitrogen (N) availability index at the three study sites.

	N availability index (μg/g air-dry resin)		
Site	NH_4^+	NO_3^-	$NH_4^+ + NO_3^-$
Cascade Head	99.0 (59.1)*a*	8.1 (9.7)*a*	107.1 (59.1)*a*
H.J. Andrews	19.1 (8.1)*b*	2.8 (0.7)*a*	21.8 (7.8)*b*
Pringle Falls	19.1 (17.5)*b*	10.0 (6.3)*a*	29.1 (21.5)*b*

Note: Values are means with SEs in parentheses. Values in a column followed by a different letter are significantly different ($P < 0.05$).

Abiotic factors and different decomposition environments

The global gradient of increasing soil organic matter with increasing latitude strongly indicates that here is a control of temperature and moisture over decomposition (Schlesinger 1996). However, observable site differences (including temperature, precipitation, and soil N availability) did not lead to significant differences in fine-root decomposition in our study. This suggests that perhaps the offsetting effects of high moisture and low temperature at the coastal and inland sites, respectively, account for the lack of significant site effects on decomposition. The lack of site effects may also be ascribed to the buffering role of soil in reducing the fluctuations of soil thermal and moisture conditions at the three sites.

The environmental factors that potentially limit decomposition appear to have varied with sites. Therefore the effects of these factors on decomposition could be offset. Although the coastal site showed the most favorable thermal conditions among the three sites (Fig. 2), the moisture content of dead roots at that site usually ranged from 300 to 400% (Fig. 3), a level that could hinder the decomposition of roots (Chen 2000). Soil temperature at the dry PRF site could reach as low as 1°C in winter and early spring (Fig. 2), and this cold period lasted several months and would have slowed root decomposition (Chen et al. 2000).

Soils play a buffering role, to some degree, in reducing the extremes of soil temperature and root moisture, and this might explain the lack of site effects on the decomposition of fine roots. Yearly fluctuations in soil temperature were considerably less than those in air temperature (Chen 1999), although the differences in soil temperature among the three sites were still substantial (Fig. 2). The annual precipitation at PRF was only 15% of that at CAH and 22% of that at HJA. Despite this, decomposing roots were not as dry as we had expected at PRF, as they stayed above 100% moisture content all year round (Fig. 3). In a laboratory experiment, a moisture content of 100% did not significantly limit root decomposition (Chen et al. 2000).

In this study, we used litter bags made of dacron cloth with a fine mesh size (50 μm) to prevent the physical loss of root particles. Litter bags may underestimate root decomposition rate constants and this may have resulted in the lack of significant site effects on root decomposition. Large soil organisms may have been excluded by the mesh bags and thus consumption would be minimized and fungal colonization may have been delayed. In addition, rhizosphere organisms that could play a role in decomposition may have been killed or separated from the fine roots during sample preparation

Fig. 2. Seasonal patterns of soil temperature (20-cm depth) at the three study sites.

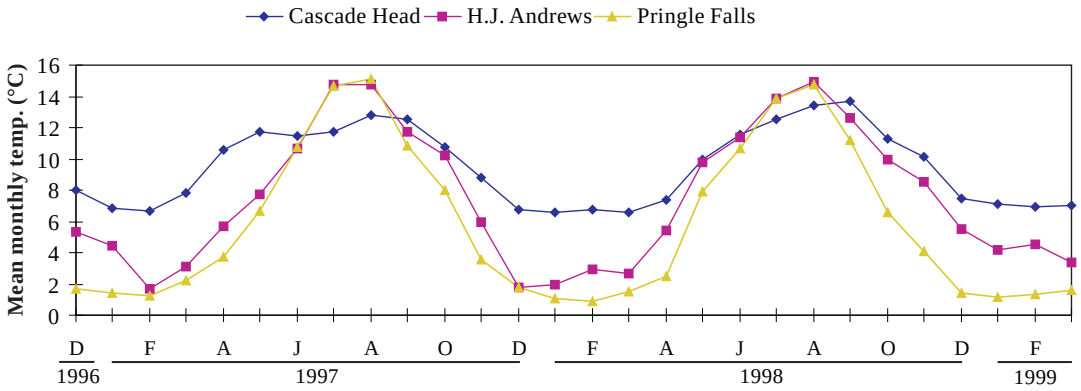
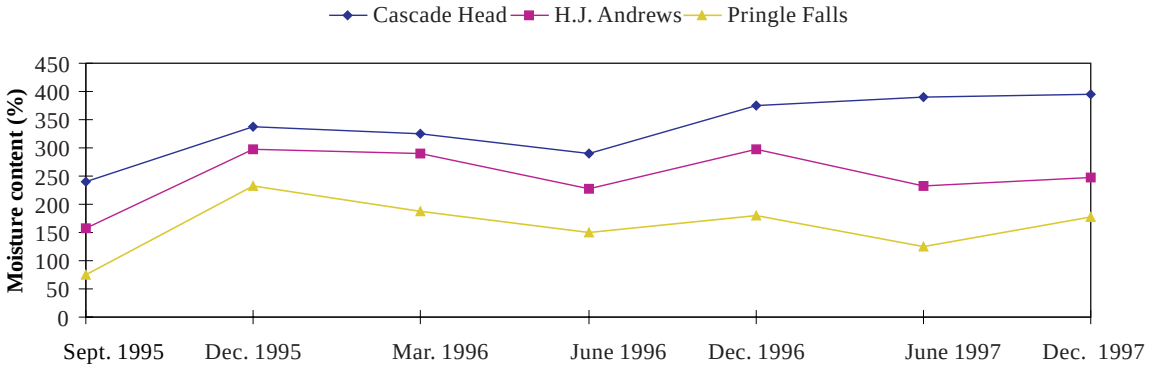


Fig. 3. Fine-root moisture content dynamics at the three study sites.



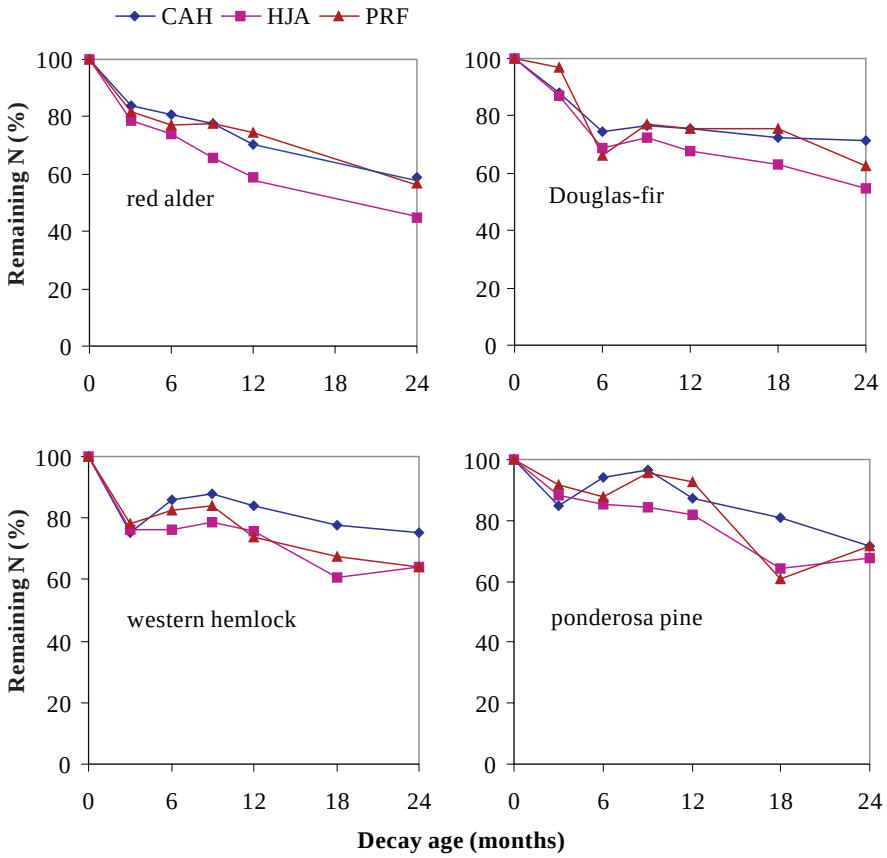
(McClaugherty et al. 1984; Fahey and Arthur 1994). Further improvement is needed to better estimate root decomposition rates. Nevertheless, litter-bag techniques are attractive in their simplicity and convenience and produce reasonably reliable results compared with trench plot techniques (McClaugherty et al. 1984) and other indirect measurements of fine-root decomposition (Santantonio and Hermann 1985; Fahey and Arthur 1994). As long as their limitations are recognized, litter-bag techniques still have an important role to play in the study of root decomposition, especially when combined with more sensitive measures such as isotope labeling.

Nitrogen dynamics

The fine roots of different species released N at different rates, depending on their initial N concentration (Fig. 5). The initial N concentration alone accounted for 80% of the variation in the rate of N release. Moreover, we can calculate the mean threshold value of initial N concentration at which the fine roots either release or accumulate N during decomposition (Fig. 5). This value of initial N concentration is, on average, 0.4% of the dry mass, indicating that as long as the initial N concentration of fine roots was higher than 0.4%, roots would release N during 2 years of decomposition. Our roots were from nursery seedlings and the initial N concentration of fine roots, ranging from 0.9 to 2.2%, was much higher than 0.4%. Therefore, it was not surprising that the decomposing roots released N in our experiment.

Nitrogen immobilization in decomposing roots was expected because of N limitation in the coniferous forests of the Pacific Northwest. Nutrient-limited ecosystems often exhibit patterns that enhance nutrient conservation such as increased nutrient immobilization during litter decay (Conn and Day 1997; Hobbie 2000). Decomposing fine roots released N during the earliest decomposition stages across all three sites with differing soil N availability, indicating little effect of soil N availability on N dynamics of decomposing roots. The N release pattern observed in this study is in agreement with several other field root decomposition studies (Seasted et al. 1992; Conn and Day 1997; Kings et al. 1997). Seastedt et al. (1992) reported very low N immobilization potential for tallgrass prairie roots. The dead roots, with an initial N concentration of 0.49%, released about 40% of their original N content during the first 2 years of decomposition in their study. Kings et al. (1997) found that the N content of small roots (<5 mm in diameter, 0.6% initial N concentration) decreased to approximately 50% of the original content after 2 years of decomposition in loblolly pine (*Pinus taeda* L.) forest. However, our results contrast with the high levels of N immobilization in roots in Hawaiian forests (Ostertag and Hobbie 1999). Ostertag and Hobbie (1999) found that decomposing fine roots immobilized up to 2.6 fold of the initial N content after 1 year of decomposition in Hawaiian montane forests with differing soil nutrient availability. The range of initial N concentration of the fine roots examined in that study was from 0.31 to 0.61%, much lower than the initial N concentration of the fine roots in this study. More studies are needed to test whether the low N immobilization potential of root detritus we observed holds true in other terrestrial ecosystems.

Fig. 4. Nitrogen dynamics in fine-root decomposition at the three study sites in the four backbone species.



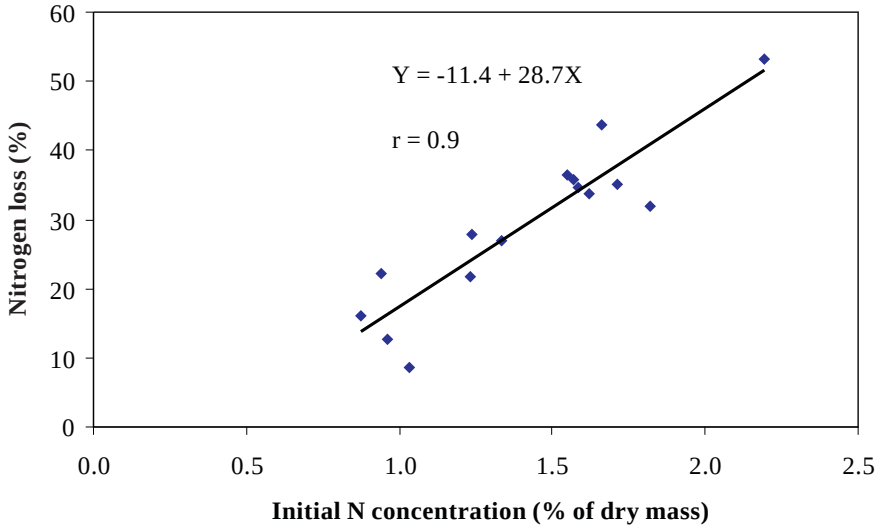
Fire and clear-cut harvesting have been the primary disturbance agents in the coniferous forests of the Pacific Northwest (Garman et al. 1999), causing a substantial mass of fine roots to die. Also, the production, mortality, and decomposition of fine roots are important natural processes in these forests (Santantonio and Hermann 1985). Our results indicate that decomposing fine roots can be an important N source in disturbed as well as undisturbed forests. After a clearcut or catastrophic forest fire, an average of 10 Mg/ha of dead fine root biomass is created in mature Douglas-fir forests (Vogt et al. 1986). The mortality rate of fine roots was about 6 $Mg \cdot ha^{-1} \cdot year^{-1}$ in undisturbed mature Douglas-fir forests, assuming that root mortality is equal to root production (Santantonio and Hermann 1985). We assumed that Douglas-fir and western hemlock accounted for 60 and 40%, respectively, of these roots. Using the data from our study, we estimated that about 33 kg N/ha would be released from the decomposing fine roots in the first year after a clearcut or catastrophic fire in mature Douglas-fir forests, although the rate of N release from the decomposing roots is expected to decrease in the second year. For undisturbed Douglas-fir forests, 20 kg N/ha annually would be released from the chronic fine-root turnover based on our estimate. Moreover, this rate of N release is likely stable over time, unlike the decrease after catastrophic disturbance. This N release from the fine roots is a large N input compared with other N sources in these forests. For example, annual N input from precipitation and dust is 2.0 kg/ha; 2.8 kg/ha are fixed by cyanophycophilous lichens in the canopy; and 14.1 kg $N \cdot ha^{-1} \cdot year^{-1}$ are returned to the forest floor by aboveground litterfall (Sollins et al. 1980). Nitrogen from decomposing fine roots may be important for the sustainable development of Douglas-fir forests in the Pacific Northwest because it may aid forest growth after cata-

Table 8. Nitrogen release from the decomposing fine roots after 1 and 2 years of field incubation at the three study sites.

	1 year		2 years	
Species	Mean (%)	SE	Mean (%)	SE
Douglas-fir*	27.0	4.5	37.2	8.5
Red alder*	32.0	8.1	46.4	7.4
Ponderosa pine*	12.7	5.3	29.6	2.2
Western hemlock*	22.2	5.3	32.1	6.5
Bigleaf maple	36.5	8.2	55.3	2.8
California red fir	34.7	3.3	51.1	5.1
Engelmann spruce	27.8	5.6	38.7	6.0
Incense-cedar	8.7	4.7	26.1	5.1
Lodgepole pine	43.6	6.0	50.1	4.4
Noble fir	35.0	8.2	46.2	10.0
Nut pine	16.0	6.0	35.3	17.5
Oregon ash	21.7	6.2	44.8	1.2
Red maple	53.3	5.2	63.1	5.4
Western redcedar	33.7	6.0	48.8	10.4
White fir	35.8	7.1	49.7	6.1

Note: The mean value of N release is the mean of 12 samples from the three sites. Asterisks indicate the backbone species. SE, standard error.

Fig. 5. Relationship between the initial N concentration and N loss in fine roots after 2 years of decomposition.



strophic disturbance, provided that regeneration after a clearcut or fire is rapid. However, if tree species do not regenerate quickly, the N released from the fine roots might be lost from the system.

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