# Decomposition and nitrogen release from decomposing woody roots in coniferous forests of the Pacific Northwest: a chronosequence approach

**Hua Chen, Mark E. Harmon, and Robert P. Griffiths**

**Abstract**: Decomposition of woody roots in Sitka spruce (*Picea sitchensis* (Bong.) Carrière), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and ponderosa pine (*Pinus ponderosa* P. Laws. ex C. Laws.) dominated forests in Oregon, U.S.A. was studied using a chronosequence. Roots of five coniferous species were excavated from stumps with ages up to 46 years old. In order of increasing decomposition rate constant (*k*) the species were Douglas-fir < Sitka spruce < lodgepole pine (*Pinus contorta* Dougl. ex Loud.) < western hemlock (*Tsuga heterophylla* (Raf.) Sarg) < ponderosa pine. Variation in the proportion of bark, wood, and resin cores was correlated to these differences. Root wood showed the highest *k*, root bark the second, and resin cores the lowest. The occurrence of resin cores in woody roots of Douglas-fir, Sitka spruce, and lodgepole pine greatly slowed the decomposition of these species. White rots occurred frequently in ponderosa pine and lodgepole pine, whereas brown rots mostly appeared in Douglas-fir and Sitka spruce. Species with white rot had a higher *k* than those with brown rot. Decomposing woody roots started to release N after 20–30% mass loss, a point when the dead root C/N ratio averaged 140.

**Résumé** : La décomposition des racines lignifiées a été étudiée à l'aide d'une chronoséquence dans les forêts dominées par l'épinette de Sitka (*Picea sitchensis* (Bong.) Carrière), le douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) et le pin ponderosa (*Pinus ponderosa* P. Laws. ex C. Laws.) en Oregon, aux États-Unis. Les racines de cinq espèces de conifères ont été excavées chez des souches dont l'âge pouvait atteindre 46 ans. Le classement des espèces par ordre croissant de la constante du taux de décomposition (*k*) était le suivant : le douglas de Menzies < l'épinette de Sitka < le pin lodgepole (*Pinus contorta* Dougl. ex Loud.) < la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) < le pin ponderosa. La variation dans la proportion d'écorce, de bois et de moelle imprégnée de résine était corrélée avec ce classement. Le bois des racines avait la valeur de *k* la plus élevée, l'écorce venait en seconde place et la moelle imprégnée de résine avait la valeur la plus faible. La présence de moelle imprégnée de résine dans les racines lignifiées du douglas de Menzies, de l'épinette de Sitka et du pin lodgepole a grandement ralenti la décomposition de ces espèces. Des caries blanches étaient souvent présentes chez le pin ponderosa et le pin lodgepole tandis qu'il y avait surtout des caries brunes chez le douglas de Menzies et l'épinette de Sitka. Les espèces avec une carie blanche avaient une valeur de *k* plus élevée que les espèces avec une carie brune. Les racines lignifiées en décomposition commençaient à relâcher le N après une perte de masse de 20–30%, alors que le rapport C/N des racines mortes était en moyenne de 140.

[Traduit par la Rédaction]

## Introduction

Roots are important structural and functional components of forested ecosystems (Harris et al. 1977, 1980; Hermann 1977; Grier et al. 1981). A large amount of forest production is allocated to roots, resulting in a large flux of C and nutrients into the belowground system (Persson 1979, 1980; Vogt et al. 1986; Kurz et al. 1996; Cairns et al. 1997). In coniferous forests, root biomass is an especially large fraction of total stand biomass (Vogt et al. 1986; Nadelhoffer and Raich 1992). However, decomposition of woody roots and their related N dynamics has not been studied frequently, in part because of the general technical difficulty in studying belowground processes (Yavitt and Fahey 1982; Vogt et al. 1986; Fahey et al. 1988; Fahey and Arthur 1994; Heal et al. 1997).

Litter decomposition is profoundly influenced by litter substrate quality, climatic environment, and the decomposer community (Swift et al. 1979; Heal et al. 1997). Of the various indices of initial substrate quality, lignin/N and C/N ratios seem to be the best predictors of litter decomposition, especially for fine litter (Fogel and Cromack 1977; Melillo et al. 1982; Berg 1984; Hobbie 1996). However, decomposition of dead wood is only grossly similar to fine litter (Harmon and Chen 1991). These indices have potential limitations in predicting woody root decomposition. First, the woody roots of different species do not exhibit the apparent differences in lignin/N and C/N ratios observed in fine litter, making it difficult to use these indices to predict woody root decomposition. Second, the values of these indices are quite

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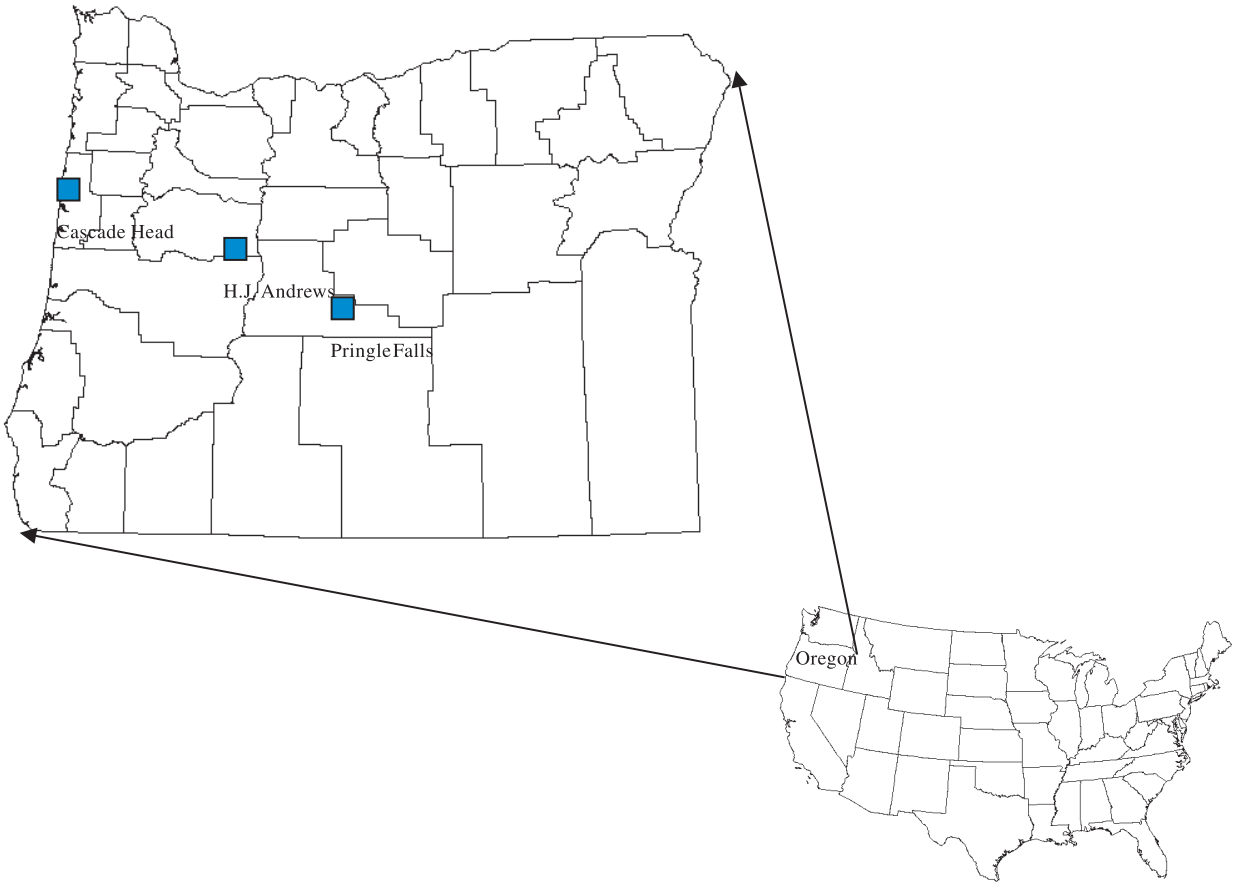
**Fig. 1.** Locations of the three study sites.




different from those of fine litter and in a range where minimal response is expected (Harmon et al. 1990). Third, the control of substrate litter quality on decomposition changes over time. Berg and Staaf (1980) found a shift from nutrient control in the early decomposition stages of *Pinus sylvestris* L. needle decomposition to the dominance of lignin in later stages.

A structural component-oriented approach may provide a better solution to predicting the long-term woody root decomposition than that provided by initial substrate quality indices. This approach examines the decomposition of different components of woody roots separately to predict whole root decomposition. Various species show apparent qualitative and quantitative differences in root structural components (Yavitt and Fahey 1982; Fahey et al. 1988). Woody roots are comprised of bark, wood, and in some cases, a resin core analogous to knots in tree boles. These components, varying with species and root sizes, appear to decompose at different rates.

We hypothesized that, for a particular size class, differences in the woody root decomposition rate constants ($k$) among species would be explained by their structural component composition, especially the presence of resin cores. From this we predicted the decomposition of woody roots with resin cores would be slower than that of woody roots without resin cores. Moreover, $k$ should decline with increasing root diameter because of a higher volume/surface area ratio, the greater amount of time required for fungal colonization of larger diameter roots, and an increasing proportion of resin cores (Fahey et al. 1988). Finally we predicted that because of the high initial C/N ratio, decomposing woody roots would initially experience a long N accumulation period and then release N gradually during the later decomposition stages. We tested these hypotheses by sampling woody roots from chronosequences of stumps created by timber harvest and thinning in Oregon, U.S.A.

## Study sites

This study was conducted at three sites: the Cascade Head Experimental Forest (CAH), H.J. Andrews Experimental Forest (HJA), and Pringle Falls Experimental Forest (PRF) (Fig. 1). These three sites form a climatic gradient from warm and wet at CAH to cool and dry at PRF. Two dominant coniferous species were chosen at each site. They were Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg) at CAH; Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock at HJA; and ponderosa pine (*Pinus ponderosa* P. Laws. ex C. Laws.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) 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. Soils are silt loams to silt clay loams derived from marine silt stones, moderately well drained, and high in organic matter and N concentration. The dominant forest type is a mixture of western hemlock and Sitka spruce (Franklin and Dyrness 1973). HJA is located 80 km east of the city Eugene, Oregon on the west slope of the Cascade Range. The cli-

mate 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 20–60%. 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 of 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 aerial deposited dacite pumice. Topography is rolling to gentle slopes. The dominant forest type is a mixture of ponderosa pine and lodgepole pine (Franklin and Dyrness 1973).

## Methods

### Stand selection

One chronosequence of commercially thinned and clear-cut stands was located at each site. Current stand vigor and locations, as well as thinning or cutting ages, were considered during stand selection. Vigorous forest stands indicated, to some degree, that the previous stands were healthy and the chance of root rot was small. All sampled stands at each site were close to each other and similar in elevation, topography, and soil type. At CAH, the chronosequence included seven stands. Of these stands, woody roots of Sitka spruce were taken from trees that were cut or thinned 7, 20, 33, 37, and 46 years prior to sampling. Root samples of western hemlock were obtained from trees cut 2, 7, 10, 16, 20, 33, and 37 years prior to sampling. The second chronosequence, located in the western hemlock zone (300–1550 m elevation) at HJA, included eight different stands. Of these stands, woody roots of Douglas-fir were taken from trees that were cut or thinned 8, 10, 14, 21, 31, 36, 40, and 45 years prior to sampling. Root samples of western hemlock were obtained from trees cut 8, 10, 14, 25, 31, and 36 years prior to sampling. The third chronosequence was located at PRF, where ponderosa pine roots were sampled at six stands. Woody roots of ponderosa pine were sampled from trees that were cut or thinned 4, 7, 10, 19, 22, and 25 years prior to sampling. Lodgepole pine roots were obtained from trees cut 7, 10, 16, 19, 22, and 28 years prior to sampling. Samples of undecayed woody roots from fresh uprooted trees of these species were sampled to serve as controls.

### Root excavation and density determination

Five stumps were selected for root excavation for each species at each stand. We avoided the stumps with a "healing bump" on the their surface, suggesting the roots of these stumps continued to live for some time. This phenomenon occurred occasionally on small stumps (diameter <15 cm) of western hemlock at the coastal site and the H.J. Andrews site. However, it was very rare among the bigger stumps of the five species we examined. Thus, the assumption that woody roots started decomposing upon cutting is reasonable for the stumps we chose. Woody roots (diameter >1 cm) were collected by excavating the root systems of chosen stumps at each stand in the summer of 1995 and 1996. After excavating the soil surrounding the roots, 10–20 cm long samples were removed using a handsaw, reciprocating saw, or in the case of very large roots, a chainsaw. Three to fifteen root samples were harvested from each stump. These roots were sorted into two size classes: small roots (diameter 1–5 cm) and large roots (diameter 5–10 cm, occasionally up to 15 cm). After removal, the dimension of each root sample was recorded in the field, including the average outermost diameter, the average longitudinal length, average bark thickness, and bark cover in percent. Each average was based on the mean of three measurements. Then the average root wood diameter and longitudinal length were recorded after removing the bark. If a resin core was present, its length and diameter were measured after separating it from the wood. Bark cover was estimated visually, or if this was not possible, we measured the entire bark surface area by forming bark pieces into a regular shape such as a rectangle. For very old decomposed roots, bark could not be recovered completely during root excavation. However, this occurred rarely and the results of bark decomposition should not be influenced significantly.

The whole volume of each root was calculated from the formula for a cylinder:

$$V = \pi \frac{(D^2 L)}{4}$$

where $V$ is the volume, $D$ is the average outermost diameter, and $L$ is the average longitudinal length. The root wood volume was calculated by the same formula using average root wood diameter instead of average outermost diameter if resin cores were not present. The bark volume of roots was based on the difference between the volumes of whole roots and root wood. If resin cores were present the volume of root wood was the difference of the entire root wood (including resin cores) volume and the resin core volume. In comparison with a water displacement method, our method of measuring the volume of root samples gave similar results, but was much more efficient. Finally, the presence of brown vs. white rots associated with the decomposing wood was visually evaluated and recorded in the field. The affected wood attacked by brown rots develops a brown color. The affected wood attacked by white rots is usually white or grayish-white in color, but it may assume various shades of yellow, tan, and light brown (Panshin and Zeeuw 1980).

Root samples were dried to a constant mass at 65°C and weighed at the laboratory. Densities of bark, wood, and resin cores of each individual root sample were calculated as the ovendry mass divided by its green volume. The density of whole roots was obtained based on the density of each component and their proportion of total volume. Decomposition of woody roots was estimated from changes in ash-free density of root components. Dried root samples were ground in a Wiley mill and passed through a fine screen (1 mm). Samples were stored in 20-mL vials to prevent moisture changes prior to analyses for ash, N, and organic constituents.

### Wet chemistry analyses

All the root samples were scanned using a Near Infrared Reflectance Spectroscopy (NIRS) Systems 6500 analyzer to predict ash and N concentrations (Chen 1999). The NIRS calibration of ash and N was conducted separately for each site using the ash and N concentrations of woody roots obtained from wet chemistry analyses. The details of the calibration and prediction are described by Chen (1999). Nitrogen concentration of whole roots was calculated using the concentrations of components and fractions of components. All the density and N values reported in this paper are ash-free values.

We analyzed ash and N concentrations of the selected root samples at the Soils Laboratory of Forest Science, Oregon State University. Ash concentration of 502 root samples was determined by heating in a muffle furnace at 500°C for 4 h. Nitrogen concentration of 121 root samples was measured by the micro-Kjeldahl technique, with the digestate analyzed by automated solution chemistry procedures (Alpkem Rapid Flow Analyzer 300 series) (McClaugherty et al. 1985). In addition, 47 root samples were measured by Carlo Erba C/N analyzer for C and N concentrations. Cross-laboratory comparisons have shown that these two techniques for measuring N concentration are equivalent (C. Glassman, personal communication).

The organic constituents of fresh small (1–5 cm) and large (5–10 cm) roots of Douglas-fir, western hemlock (HJA), ponderosa pine, and lodgepole pine were analyzed to determine initial substrate quality. The constituents analyzed included nonpolar extractives (NPE: fats, oils, and waxes) using dichloromethane as the extractant (TAPPI 1975), hot water soluble phenols (Folin–Denis method, Allen et al. 1974), 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 this as "lignin." All organic constituents are reported as a percent of ash-free dry mass.

### Statistical analysis

The single-exponential model was used to estimate *k* value of roots (Yavitt and Fahey 1982; Bloomfield et al. 1993). The assumption that decomposition is proportional to the amount of material remaining leads to the model

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

where $Y_0$ is the initial quantity of material, $Y_t$ is the amount left at time $t$, and $k$ is the decomposition rate constant. For our purposes, density was used as the $Y$ variable. For bark, wood, resin cores of roots, and whole roots, $k$ values were calculated from the linear regressions of the mean remaining density of the structural component, transformed into natural logarithms (ln) vs. time. The slope of these regressions was $k$.

In addition, a double-exponential model was fitted using nonlinear regression for the species with resin cores:

$$Y_t = Y_{\text{slow}}\ e^{-k_s t} + Y_{\text{fast}}\ e^{-k_f t}$$

where $Y_{\text{slow}}$ is the relative density of recalcitrant fraction of roots such as resin cores, $Y_{\text{fast}}$ is the relative density of fast decomposing proportion of roots, $Y_t$ is the remaining density of woody roots at time $t$, and $k_f$ and $k_s$ are the decomposition rate constants of fast and slow decomposing fractions of roots, respectively.

In our study, we compared the confidence intervals of the estimated $k$ values of root components and whole roots. There is a fairly close relationship between the overlap in the confidence intervals and the significance of a test of equal means (Jongman et al. 1995).

All statistical tests were performed by the GLM and NLIN procedure of SAS (SAS Institute Inc. 1985). Statistical tests were significant if $0.05 > P > 0.01$ and highly significant if $P \leq 0.01$.

## Results

### Decomposition of structural components

*Density changes over time*

Density changes were different among the various root components (Fig. 2). The rate of mass loss of root wood was faster than that of root bark. The density of resin cores showed no significant declining trend, even after 40 years of decomposition. Highly decomposition-resistant resin cores occurred mainly in Sitka spruce, Douglas-fir, and lodgepole pine. Declines in bark densities of small roots were similar to those of large roots in most species. That was also true for wood density of small roots and large roots.

*k value of root components*

Different root components showed clearly different *k* values (Table 1), with that of wood being the highest, ranging from 0.030 to 0.111 per year. One exception was for small lodgepole pine roots, which had a wood decomposition rate similar to that of bark. The *k* value of root bark was intermediate, ranging from 0.011 to 0.044 per year, while resin cores showed the lowest *k* value by an order of magnitude (0.000 to 0.004 per year). Comparisons of *k* confidence intervals indicated that the *k* value of root wood was significantly higher than that of root bark for ponderosa pine, although this significant relationship did not hold for the other species (Fig. 3).

When the same root component was compared, species in the three sites differed in *k* value (Fig. 3). Of the five species examined, the root wood of ponderosa pine showed the highest *k* value (0.103–0.111 per year), although the *k* values of root wood in the other four species were not statistically different. When comparing small root wood decomposition, Douglas-fir had the lowest rate constant with a value of 0.030 per year. Comparing the *k* value of root bark (regardless of root size) among the species, lodgepole pine had highest *k* value, ranging from 0.039 to 0.044 per year. In contrast, the *k* value of root bark of Sitka spruce large roots was the lowest at only 0.011 per year. Although the *k* value for lodgepole pine bark was higher than that of the other species, it was only significantly different from the root bark of Douglas-fir small roots.

*Rot types of root wood*

The type of rot present varied with species. White rots were most frequent in the decomposing wood of ponderosa pine and lodgepole pine (84–79%) (Fig. 4). In contrast, brown rots were most frequently found in woody roots of Douglas-fir and Sitka spruce (56% and 72%, respectively). White rots and brown rots both occurred in decomposing western hemlock roots at CAH and HJA site.

### Decomposition of whole roots

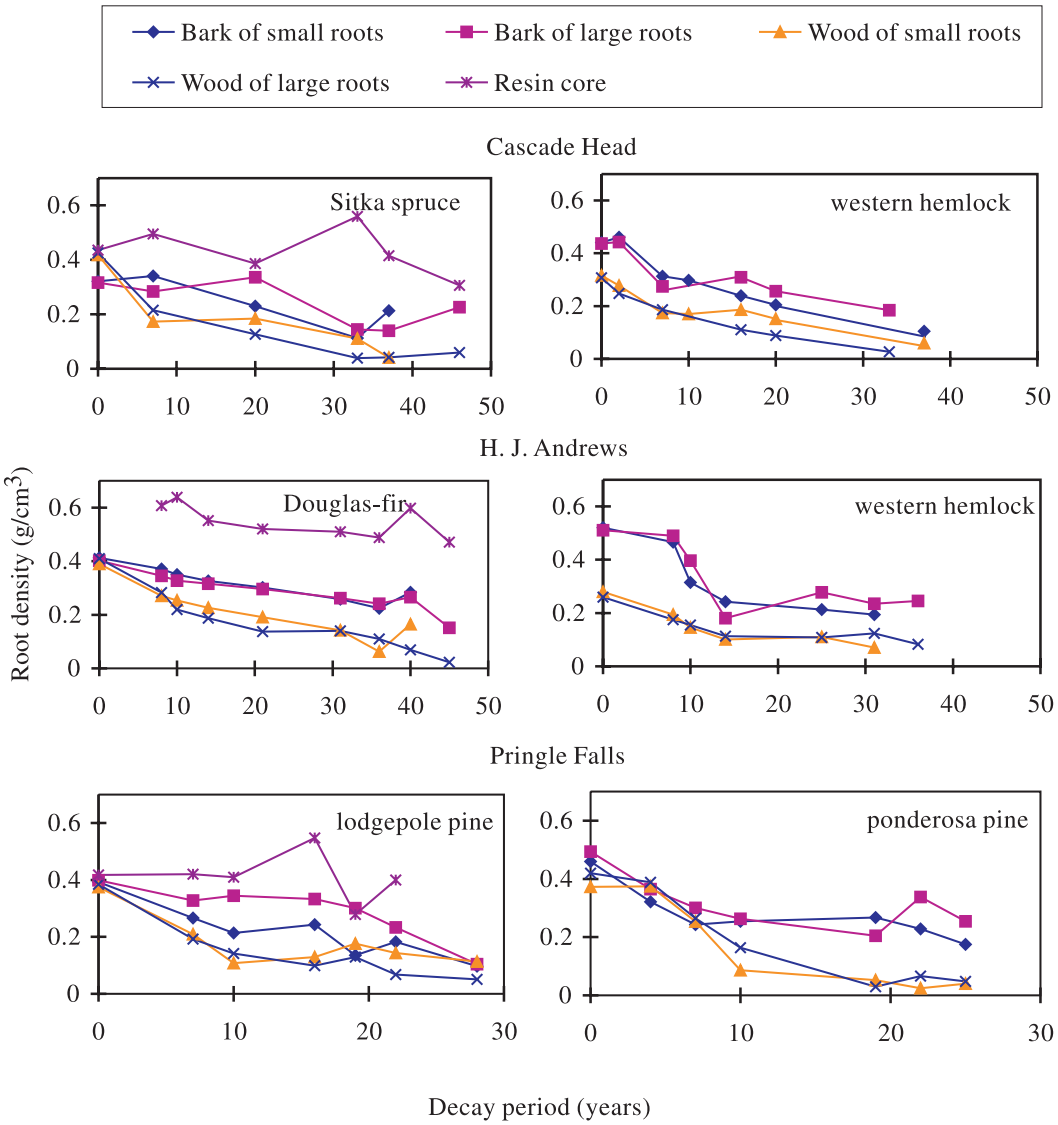
*Density changes over time*

Species separated into two major root decomposition patterns over time. For lodgepole pine, Douglas-fir, and Sitka spruce, the species with resin cores, the density of whole roots decreased in the early decomposition stage and then tended to remain constant as decomposition progressed (Fig. 5). In contrast, root density of western hemlock and ponderosa pine continually decreased until all the components of roots were decomposed (Fig. 5).

*Controls of resin cores and bark*

Lodgepole pine, Douglas-fir, and Sitka spruce had a high frequency of resin core occurrence in woody roots, ranging from 56 to 76%, compared with the 7 and 11% frequencies of resin cores in western hemlock and ponderosa pine (Table 2). The high proportional volume of resin cores in the former species group also made a critical contribution to the decomposition resistance of their roots. Roughly 30% of the whole root volume among lodgepole pine, Douglas-fir, and Sitka spruce was resin cores. Moreover, resin cores could be found in woody roots as small as 2 cm in diameter, although most resin cores occurred in woody roots larger than 5 cm in diameter. The differences in bark volume among these species also contributed to the two distinct decomposition pat-

**Fig. 2.** Density change of the different root components of five species at three sites.




terns of woody roots. Species having slow rates of density change in later decomposition stages had a high proportion of bark (Table 2 and Fig. 5). These species included Sitka spruce and Douglas-fir. Western hemlock and ponderosa pine, which showed a steady decrease in root density, contained a small fraction of bark in their roots.

*k value of whole roots*

Woody roots of Sitka spruce, Douglas fir, and lodgepole pine with resin cores had lower *k* values than those of western hemlock and ponderosa pine without resin cores (Table 3). The *k* values of Sitka spruce, Douglas fir, and lodgepole pine woody roots were 0.016–0.021, 0.011–0.013, and 0.025–0.030 per year, respectively. In contrast, western hemlock and ponderosa pine had higher *k* values, ranging from 0.033–0.049 to 0.073–0.077 per year. There were significant differences in the *k* value of woody roots among the species even when root size was similar ($F = 10.13$, $P < 0.05$) (Fig. 6). The order of increasing woody root *k* value was Douglas-fir < Sitka spruce < lodgepole pine < western hemlock (HJA) < western hemlock (CAH) < ponderosa pine. No significant differences in *k* value were observed between the two size classes (small vs. large roots) of the species examined (Fig. 6).

The double-exponential model, which accounts for fast- and slow-decomposing components separately, indicated a better fit than the single-exponential model for woody roots with resin cores (Tables 3, 4, and Fig. 7). The $R^2$ of the regressions for Sitka spruce, Douglas-fir, and lodgepole pine was above 0.93, except for a value of 0.8 for the small roots of Douglas-fir. The *k* value of the labile fraction of woody roots for these three species was 0.035–0.127, 0.035–0.087, and 0.086–0.090 per year, respectively. The *k* value of the slow decomposing fraction of woody roots ranged from 0.0001 to 0.004, at least an order of magnitude lower than the rates of the fast decomposing fraction of woody roots.

*Initial substrate quality*

No clear interspecific or size differences were observed in the initial C concentration of roots (Table 5). Initial C concentrations among the roots ranged from 50.0 to 51.8%. Large roots of western hemlock (HJA) and ponderosa pine

**Table 1.** Coefficients of regressions of the single-exponential model used to estimate the decomposition rate constant ($k$) of the root components of each species.

| Site | Species | Component | Diameter (cm) | Regression coefficients[a] | | | |
|---|---|---|---|---|---|---|---|
| | | | | $Y_0$ (g/cm$^3$) | $k$ (per year) | $R^2$ | $N$[b] |
| Cascade Head | Sitka spruce | Bark | 2–5 | 0.35 | 0.022 | 0.63 | 5 |
| | | Bark | 5–13 | 0.32 | 0.011 | 0.39 | 5 |
| | | Wood | 2–4 | 0.36 | 0.047 | 0.80* | 5 |
| | | Wood | 4–13 | 0.33 | 0.047 | 0.84* | 5 |
| | | Resin | 2–5 | 0.40 | 0.000 | 0.00 | 5 |
| | Western hemlock | Bark | 1–4 | 0.45 | 0.039 | 0.98** | 7 |
| | | Bark | 4–14 | 0.37 | 0.021 | 0.43 | 6 |
| | | Wood | 1–4 | 0.29 | 0.040 | 0.91** | 7 |
| | | Wood | 4–13 | 0.31 | 0.070 | 0.98** | 6 |
| H.J. Andrews | Douglas-fir | Bark | 2–5 | 0.40 | 0.012 | 0.82** | 7 |
| | | Bark | 5–15 | 0.40 | 0.016 | 0.79** | 8 |
| | | Wood | 2–4 | 0.36 | 0.030 | 0.69* | 7 |
| | | Wood | 4–13 | 0.42 | 0.053 | 0.88** | 8 |
| | | Resin | 2–6 | 0.54 | 0.002 | 0.15 | 7 |
| | Western hemlock | Bark | 2–4 | 0.49 | 0.033 | 0.85** | 6 |
| | | Bark | 4–15 | 0.45 | 0.021 | 0.48 | 7 |
| | | Wood | 2–4 | 0.24 | 0.039 | 0.84** | 6 |
| | | Wood | 4–13 | 0.21 | 0.042 | 0.76** | 7 |
| Pringle Falls | Lodgepole pine | Bark | 2–6 | 0.38 | 0.044 | 0.84* | 7 |
| | | Bark | 6–10 | 0.48 | 0.039 | 0.68* | 7 |
| | | Wood | 2–6 | 0.26 | 0.033 | 0.52 | 7 |
| | | Wood | 6–10 | 0.33 | 0.068 | 0.92** | 7 |
| | | Resin | 1–5 | 0.38 | 0.004 | 0.01 | 5 |
| | Ponderosa pine | Bark | 1–5 | 0.37 | 0.026 | 0.70* | 7 |
| | | Bark | 5–13 | 0.39 | 0.020 | 0.45 | 7 |
| | | Wood | 1–5 | 0.42 | 0.111 | 0.90** | 7 |
| | | Wood | 5–11 | 0.47 | 0.103 | 0.87** | 7 |

**Note:** *, $0.05 > P > 0.01$; **, $P \leq 0.01$.

[a]The regression was of the form $Y_t = Y_0\ e^{-kt}$, where $Y_t$ is the density of component at time $t$ (years), $Y_0$ is the initial density of roots, and $k$ is the decomposition rate constant.

[b]Each data point in the regression is the means of 4–15 samples.

possessed the highest C/N ratio, up to 313 and 284. Small roots of ponderosa pine had highest N concentration (0.34%) and thus the lowest C/N ratio (149).

Except for western hemlock (HJA), concentrations of water-soluble phenols were higher in small roots than in large roots. Concentrations of NPE (fats, oils, and waxes) did not have a clear pattern among different size roots. Nor did acid-hydrolyzable fraction change very much with different species and size. Lignin concentrations were relatively low in roots of ponderosa pine and high in those of Douglas-fir, and the size of roots did not show clear correlation with lignin concentration. The lignin/N ratio of these woody roots ranged from 80 to 154 (Table 5).

### Nitrogen release

Two patterns of N release existed during woody root decomposition (Figs. 8–10). The most common pattern was for N content of woody roots to show a consistent declining trend over time after a short phase of N accumulation early in decomposition (Figs. 8 and 10). Sitka spruce, western hemlock, lodgepole pine, and ponderosa pine at CAH and PRF had this pattern. A less common N dynamic appeared in both size roots of Douglas-fir and small roots of western hemlock at HJA (Fig. 9). The N content of these woody roots decreased in the early stages of decomposition, then increased during the middle decomposition period, and then the N content declined with extensive decomposition. For example, after 14 years of decomposition, the N content of Douglas-fir was 106–133% of the initial N content. Nitrogen accumulation, to a great extent, occurred in large roots of western hemlock at HJA (Fig. 9).

Nitrogen was lost from woody roots more slowly than mass (Figs. 8–10). Species differed markedly in the total net N released during decomposition, with fast decomposing species releasing more N than slow decomposing species. For example, ponderosa pine roots released almost half of their initial N during the first 25 years of decomposition. In contrast, Douglas-fir roots lost less than 20% of total initial N content during the same time period.

The trend in N release of decomposing roots was more clearly displayed by plotting the change in N content vs. mass loss (Fig. 11). Root mass loss was positively correlated with the N content loss of both species' roots at CAH ($P$ = 0.0001, $R^2$ = 0.87) and PRF ($P$ = 0.0001, $R^2$ = 0.79), using the polynomial regression

$$N_{\text{loss}} = a + bM_{\text{loss}} + cM_{\text{loss}}^2$$

where $N_{\text{loss}}$ is N loss percentage and $M_{\text{loss}}$ is the mass loss

**Fig. 3.** Decomposition rate constant for the bark and wood of decomposing roots of five species at three sites (mean ± 95% CI).

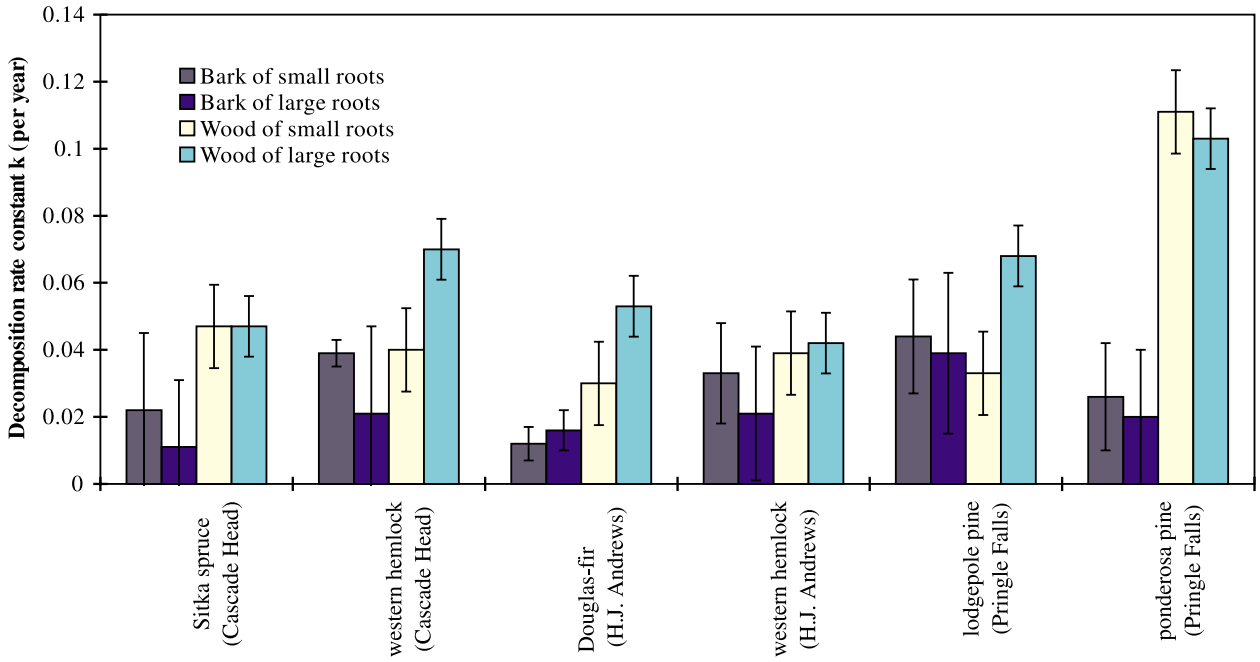
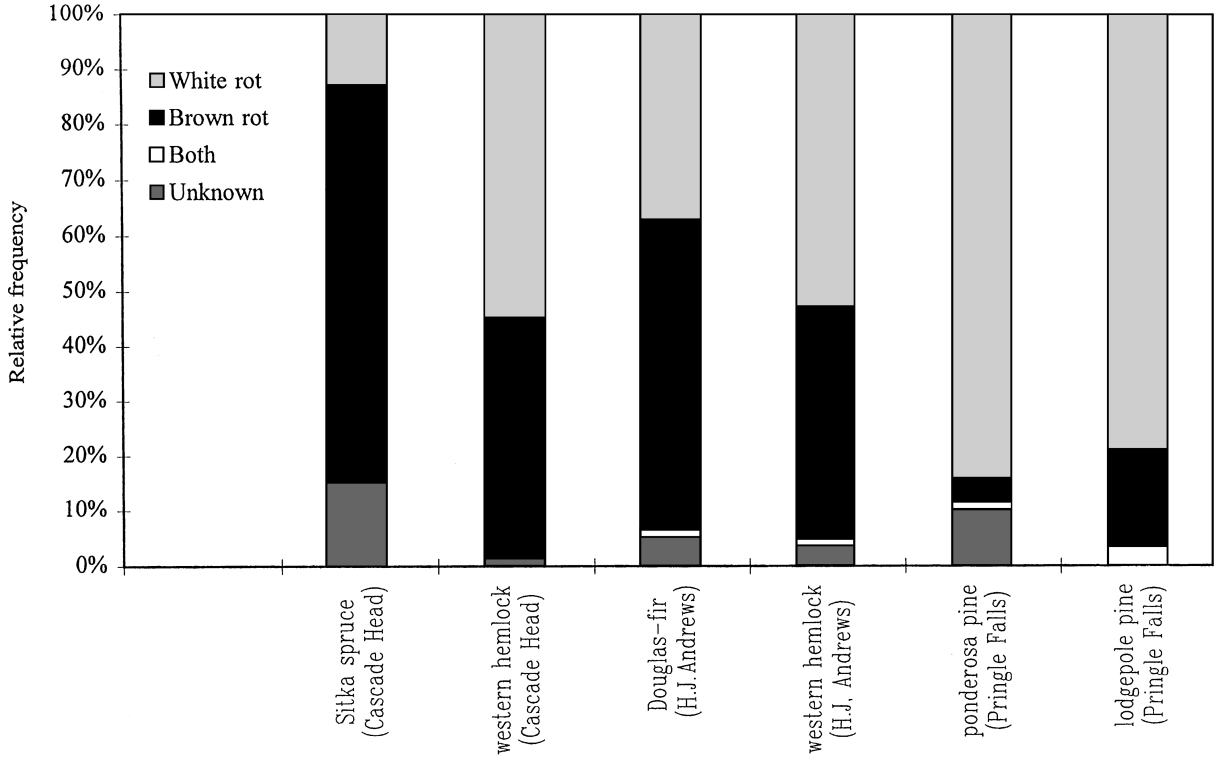



**Fig. 4.** Relative frequency of rot type in the wood component of roots.




percentage of decomposing roots. This correlation, however, was not significant at HJA ($P$ = 0.64). On an individual species basis, the polynomial model was significant for both species at CAH and PRF ($P$ < 0.02). The N dynamics of the four species at CAH and PRF clearly showed that dead woody roots released N after 20–30% of their mass decomposed. The polynomial model was not significant for either species studied at HJA ($P$ > 0.19).

Generally, the C/N ratio of decomposing root litter decreased over time, although large roots of Douglas-fir were an exception (Figs. 8–10). At CAH, C/N ratio of large woody roots of Sitka spruce dropped from 142 to 94 after 46 years of decomposition (Fig. 8). The C/N ratio of western hemlock large roots decreased from 312 to 139 at HJA (Fig. 9). Similarly, the C/N ratio of ponderosa pine large roots decreased from 284 to 104 (Fig. 10). Surprisingly, the

**Fig. 5.** Density of whole woody roots of five species at three sites.

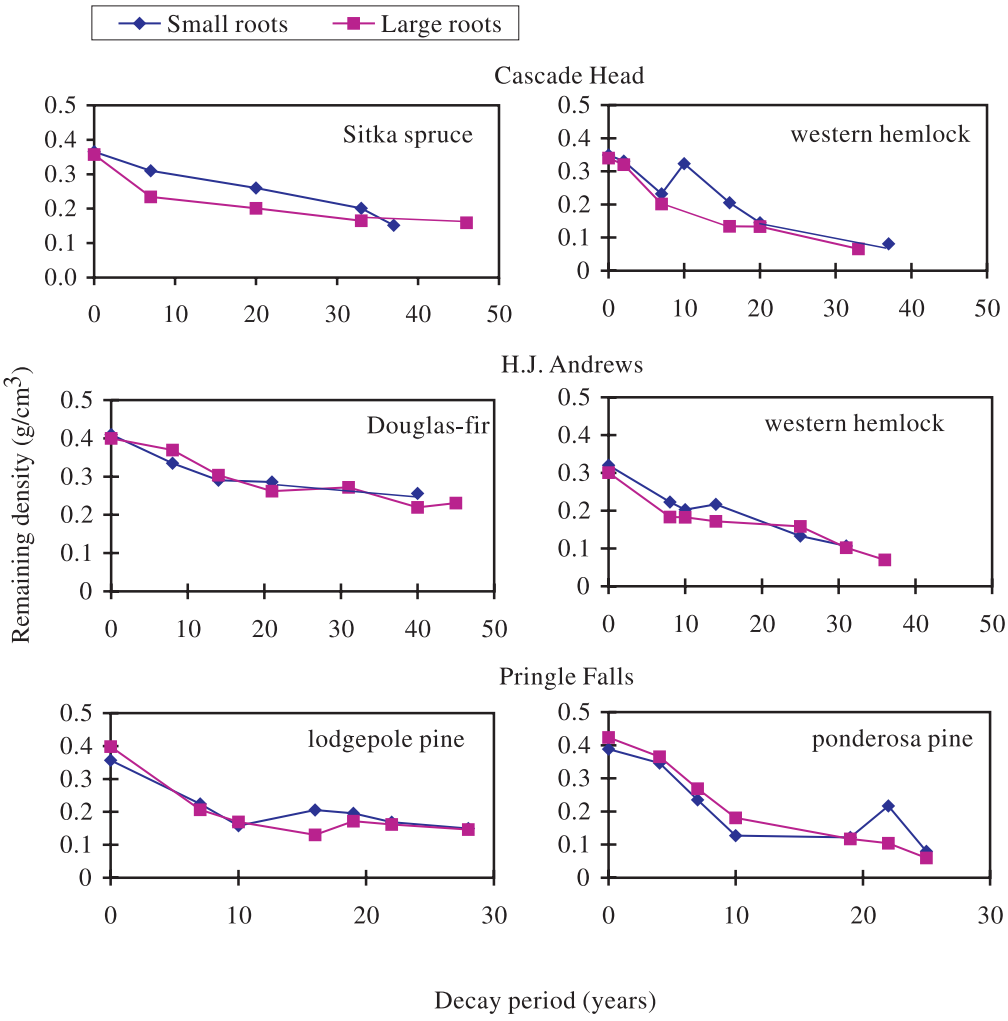



**Table 2.** Frequency and volume (%) of resin cores and volume (%) of bark in woody roots.

| | | Resin cores | | Bark |
|---|---|---|---|---|
| Site | Species | Frequency (%) | Volume in roots (%) | Volume in roots (%) |
| Cascade Head | Sitka spruce | 76 | 30.3 (13.5) | 46.5 (14.8) |
| Cascade Head | Western hemlock | 7 | 11.8 (15.3) | 28.1 (5.9) |
| H.J. Andrews | Douglas-fir | 70 | 27.2 (15.9) | 41.5 (14.7) |
| H.J. Andrews | Western hemlock | 12 | 21.2 (11.7) | 22.9 (6.9) |
| Pringle Falls | Lodgepole pine | 56 | 27.4 (16.5) | 30.7 (14.8) |
| Pringle Falls | Ponderosa pine | 11 | 10.8 (5.6) | 22.5 (10.1) |

**Note:** Values are means ± standard errors.

C/N ratio of very decomposed roots still exceeded 80 after several decades of decomposition and, despite these high values, N was released.

## Discussion

### Controls of woody root decomposition—structural components and rot types

Yavitt and Fahey (1982) suggested that sapwood and heartwood of woody roots should be examined separately to allow more accurate estimation of long-term root mass loss. Our study confirmed the importance of treating various structural components separately in estimating the long-term decomposition of woody detritus, by partitioning woody roots into bark, wood, and resin cores. Of the three root structural components, root wood showed the highest *k*; root bark the second; and the resin cores the lowest, a result that is consistent with previous studies (Fahey et al. 1988; Fahey and Arthur 1994). The decomposition of woody roots is the integrative result of the mass loss of the individual structural component of roots. The structural components of woody roots that directly influenced their decomposition pattern

**Table 3.** Coefficients of regressions of the single-exponential model used to estimate the decomposition rate constant ($k$) of the roots of dominant coniferous species in the Pacific Northwest.

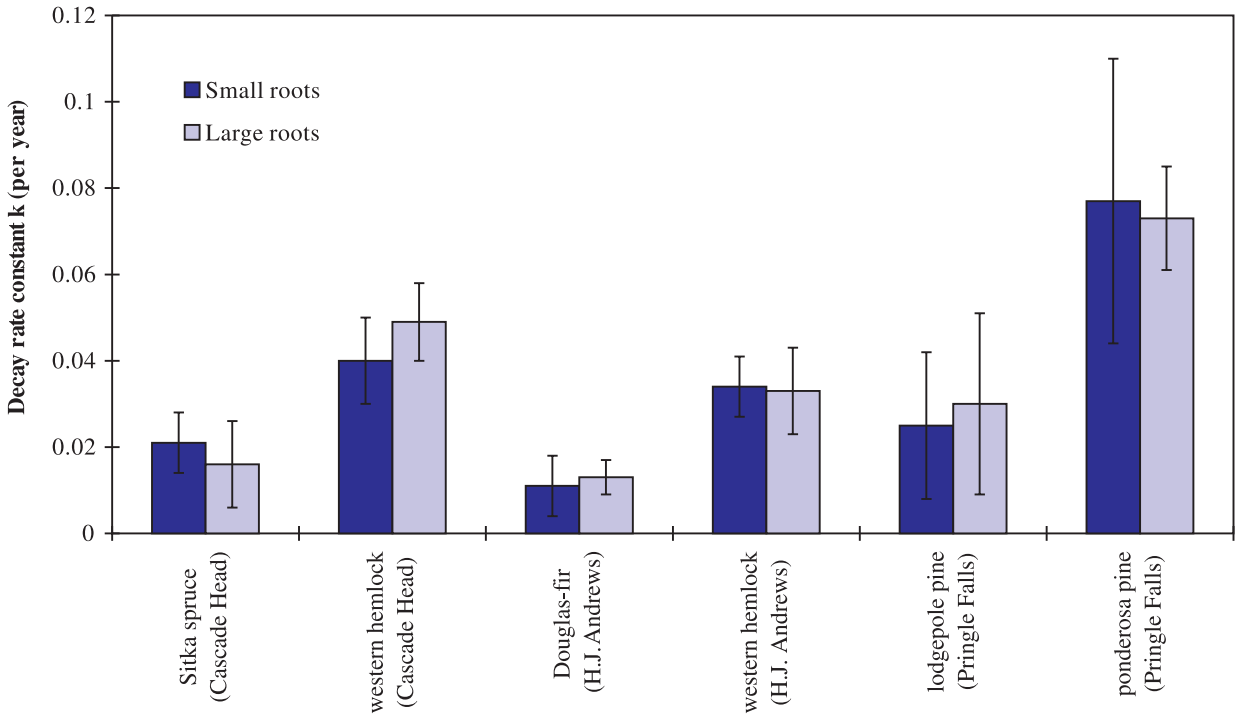
| Site | Species | Type | Diameter(cm) | Regression coefficients[a] | | | |
|---|---|---|---|---|---|---|---|
| | | | | $Y_0$ (g/cm$^3$) | $k$ (per year) | $R^2$ | $N$[b] |
| Cascade Head | Sitka spruce | Small roots | 1–5 | 0.37 | 0.021 | 0.95** | 5 |
| | | Large roots | 5–12 | 0.30 | 0.016 | 0.84* | 5 |
| | Western hemlock | Small roots | 1–5 | 0.36 | 0.040 | 0.92** | 7 |
| | | Large roots | 5–15 | 0.33 | 0.049 | 0.97** | 6 |
| H.J. Andrews | Douglas-fir | Small roots | 1–5 | 0.37 | 0.011 | 0.82* | 5 |
| | | Large roots | 5–15 | 0.39 | 0.013 | 0.90** | 7 |
| | Western hemlock | Small roots | 1–5 | 0.31 | 0.034 | 0.97** | 6 |
| | | Large roots | 5–15 | 0.27 | 0.033 | 0.89** | 7 |
| Pringle Falls | Lodgepole pine | Small roots | 1–5 | 0.29 | 0.025 | 0.64* | 7 |
| | | Large roots | 5–11 | 0.29 | 0.030 | 0.62* | 7 |
| | Ponderosa pine | Small roots | 1–5 | 0.34 | 0.077 | 0.63* | 7 |
| | | Large roots | 5–12 | 0.42 | 0.073 | 0.97** | 7 |

**Note:** *, $0.05 > P > 0.01$; **, $P \leq 0.01$.

[a]The regression was of the form $Y_t = Y_0 e^{-kt}$, where $Y_t$ is the density of roots at time $t$ (years), $Y_0$ is the initial density of roots, and $k$ is decomposition rate constant.

[b]Each data point in the regression is the mean of 3–12 samples.

**Fig. 6.** Decomposition rate constant of whole roots (mean ± 95% CI).




varied between species. In species with decomposition-resistant resin cores (e.g., lodgepole pine, Douglas-fir, and Sitka spruce), the density of whole roots decreased in the early stage because of the relatively fast decomposition of root wood and bark, then tended to remain constant as the resin cores resisted to further decomposition. The $k$ values of these species were low, ranging from 0.011 to 0.030 per year. In contrast, in species without resistant resin cores (e.g., western hemlock and ponderosa pine), root density continually decreased until all components of roots were decomposed. Moreover, these species had higher $k$ values, ranging from 0.033 to 0.077 per year. Our study suggests that the proportion of the various root structural components plays critical roles in determining the decomposition rate of a species, a factor that should be accounted for in models of woody root decomposition.

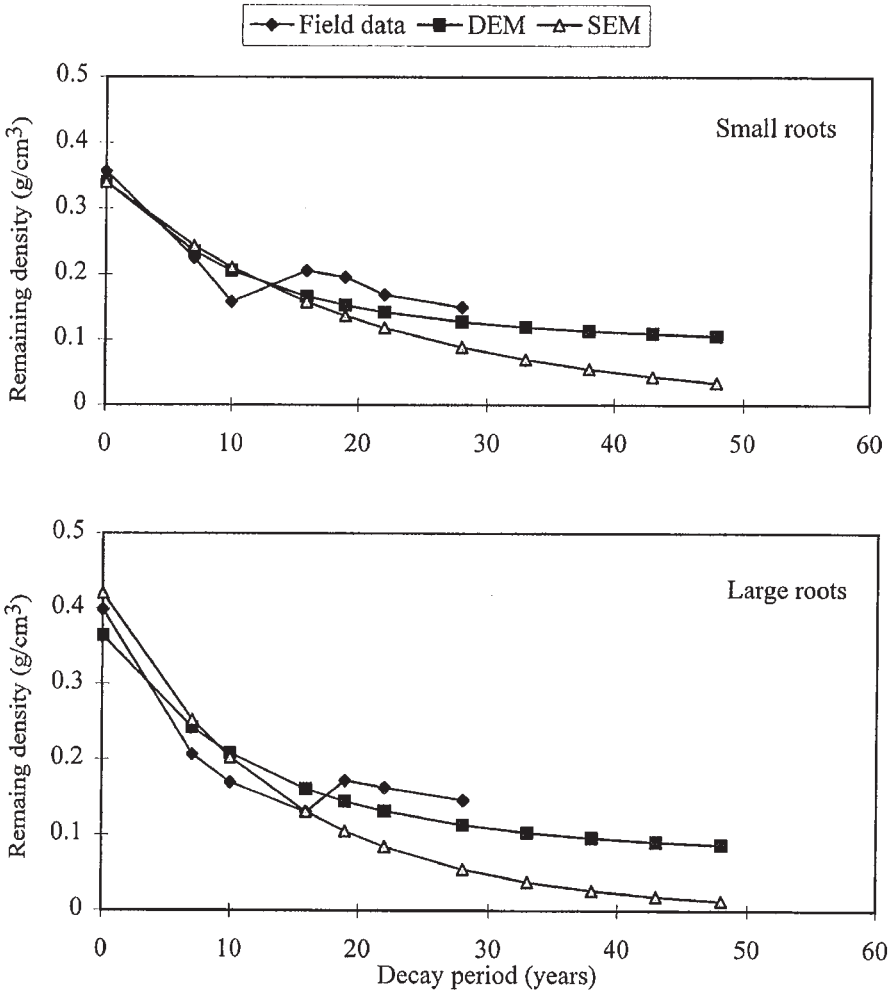
Woody roots with white rots had much higher rates of decomposition than those with brown rot. Ponderosa pine affected by white rots showed the highest $k$ values of 0.073–0.077 per year in contrast with values of 0.033–0.049 per year for western hemlock, affected by both white rots and brown rots (Table 3). Similarly, for the species with resin cores, lodgepole pine affected by white rots had higher $k$ values (0.025–0.03 per year) than those of Douglas-fir and Sitka spruce dominated by brown rots (0.011–0.013 and 0.016–0.021 per year, respectively). This is mainly due to

**Table 4.** Coefficients of regressions of the double-exponential model used to estimate decomposition rate constant of woody roots with resin cores.

| Site | Species | Type | Diameter (cm) | Regression coefficients[a] | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | $Y_{slow}$ (g/cm$^3$) | $k_s$ (per year) | $Y_{fast}$ (g/cm$^3$) | $k_f$ (per year) | $R^2$ | $N^b$ |
| Cascade Head | Sitka spruce | Small roots | 1–5 | 0.100 | 0.0001 | 0.270 | 0.035 | 0.94 | 5 |
| | | Large roots | 5–12 | 0.167 | 0.0001 | 0.188 | 0.127 | 0.98 | 5 |
| H.J. Andrews | Douglas-fir | Small roots | 1–5 | 0.253 | 0.0015 | 0.157 | 0.087 | 0.80 | 5 |
| | | Large roots | 5–15 | 0.190 | 0.0018 | 0.217 | 0.035 | 0.93 | 7 |
| Pringle Falls | Lodgepole pine | Small roots | 1–5 | 0.120 | 0.0032 | 0.220 | 0.090 | 0.97 | 7 |
| | | Large roots | 5–11 | 0.100 | 0.0040 | 0.264 | 0.086 | 0.97 | 7 |

[a]The regression was of the form $Y_t = Y_{slow}e^{-(k_s t)} + Y_{fast}e^{-(k_f t)}$ where $Y_t$ is the density of roots at time $t$ (years), $Y_{slow}$ and $Y_{fast}$ are the initial relative density of slow decomposing fraction and fast decomposing fraction of roots, and $k_s$ and $k_f$ are the decomposition rate constants of these two fractions.
[b]Each data point in the regression is the mean of 3–12 samples.

**Fig. 7.** Decay of small and large roots of lodgepole pine as measured from field data, a double-exponential model (DEM), and a single-exponential model (SEM).




white rot's capability to degrade both lignin and cellulose. In contrast, brown rots primarily attack the cellulose of cell walls, leaving behind a network consisting of modified lignin (Panshin and Zeeuw 1980; Hammel 1997). White rots frequently occurred at PRF, a site that had the lowest soil N availability among the three sites. In contrast brown rots appeared at the CAH and HJA sites that had higher soil N availability (Chen 1999). This was consistent with previous observations in which white rots were more common in soils with a low level of available N and brown rots appeared frequently in relatively high soil N availability stands (Panshin and Zeeuw 1980; Paul and Clark 1989; Hammel 1997), although the factors that determine the rot types of woody roots are not yet fully understood.

Root size did not significantly influence the $k$ value of woody roots in our study (Fig. 6). Our results are consistent with the results of Fahey and Arthur (1994), who found that root size (2–5 cm vs. 5–10 cm) had no significant effects on

**Table 5.** Chemical characteristics of fresh woody roots for two size classes.

| Species | N (%) | C (%) | C/N | NPE (%) | WS sugar (%) | WS phenols (%) | AH Cellulose (%) | ARF lignin (%) | Lignin+ cellulose (%) | Lignin/N ratio | Cellulose/N ratio | LCI ratio | (Lignin+cellulose)/N ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Small roots** | | | | | | | | | | | | | |
| Douglas-fir | 0.27 | 51.6 | 190 | 5.7 | 2.2 | 4.26 | 49.8 | 34.3 | 84.1 | 126 | 184 | 0.41 | 310 |
| Western hemlock | 0.25 | 50.8 | 202 | 2.7 | 1.4 | 4.23 | 56.6 | 31.3 | 87.9 | 125 | 225 | 0.36 | 350 |
| Lodgepole pine | 0.21 | 51.8 | 241 | 13.5 | 2.6 | 1.24 | 47.6 | 30.1 | 77.7 | 141 | 222 | 0.39 | 363 |
| Ponderosa pine | 0.34 | 51.1 | 149 | 6.0 | 2.1 | 1.93 | 58.8 | 27.5 | 86.3 | 80 | 171 | 0.32 | 252 |
| **Large roots** | | | | | | | | | | | | | |
| Douglas-fir | 0.27 | 50.9 | 187 | 1.9 | 1.4 | 2.12 | 58.3 | 32.3 | 90.5 | 119 | 214 | 0.36 | 333 |
| Western hemlock | 0.16 | 50.0 | 313 | 8.8 | 7.6 | 8.16 | 42.1 | 24.5 | 66.6 | 153 | 263 | 0.37 | 416 |
| Lodgepole pine | 0.28 | 51.6 | 183 | 7.7 | 1.3 | 0.88 | 50.0 | 36.5 | 86.5 | 130 | 178 | 0.42 | 307 |
| Ponderosa pine | 0.18 | 51.1 | 284 | 16.6 | 1.2 | 0.76 | 50.4 | 27.7 | 78.1 | 154 | 280 | 0.35 | 434 |

**Note:** NPE, nonpolar extratables (fats, oils, and waxes); WS sugar, water-soluble carbohydrate; WS phenols, water-soluble phenols, expressed as % tannic acid equivalents; AH cellulose, acid-hydrolzable cellulose and hemicellulose; ARF lignin, acid-resistant fraction including lignin and other recalcitrant carbon, referred to as lignin; LCI ratio = Lignin/(cellulose+lignin).

root decomposition of red spruce (*Picea rubens* Sarg.), American beech (*Fagus grandifolia* Ehrh.), or yellow birch (*Betula alleganiensis* Britt.) in a northern hardwood ecosystem. This probably was attributed to the similarity of root structural components of different size roots. For example, the resin cores occurred in small woody roots as well as large ones, although the volume fractions of resin cores varied with root size. The lack of size effect on root decomposition in our study might also be due to the high variability of the diameter of woody roots within each size class, which could preclude the detection of size effect on root decomposition. Our results suggest that changes in surface area/volume ratio with size and rates of fungal colonization had less influence than we had anticipated.

The single-exponential model has been used widely to model root decomposition (Yavitt and Fahey 1982; Bloomfield et al. 1993). While the decomposition rate constant calculated from this model is a useful index of decomposition, it can be misleading if the woody roots have highly decomposition-resistant resin cores (Fig. 7). The double-exponential model solves this problem by modeling both fast and slow decomposition phases. The double-exponential model produced a much better fit of the remaining density of lodgepole pine roots than the single-exponential model, especially in later decomposition stage (Table 4 and Fig. 7). Our study indicated that the single-exponential model was a good predictor of the decomposition rate constant of woody roots without resin cores. However, when resin cores were present in woody roots, the double-exponential model provided a much better long-term decomposition model.

### Nitrogen release

We hypothesized that decomposing woody roots would experience a long N accumulation process during the early decomposition stages because of their high initial C/N ratio. This phase would then be followed by a period of net N release, as observed in most fine litter decomposition studies (Gosz et al. 1973; Staaf and Berg 1981; Melillo et al. 1982; Berg and Ekbohm 1983; Aber et al. 1990). Contrary to this hypothesis, patterns of N release from decomposing woody roots at early decomposition stages at CAH and PRF were observed, consistent with those observed in several other root decomposition studies. In our study, dead roots started to release N at a C/N ratio of 140. Parker et al. (1984) found N was released in decomposing roots of a desert annual with an initial C/N ratio of 64. Seastedt et al. (1992) found dead grassland roots released N at the start of decomposition with a C/N ratio of 90. Hobbie (1996) found that several roots of Alaska tundra shrub and trees with C/N ratio of 30 to 50 lost N immediately following incubation in microcosms, although some N immobilization occurred in the later decomposition stages. These studies indicate that dead roots, unlike other litters, do not have a long N accumulation period in decomposition (Gosz et al. 1973; Staaf and Berg 1981; Melillo et al. 1982; Berg and Ekbohm 1983; Aber et al. 1990) and tend to release N at a much higher C/N ratio.

The concept of the "critical C/N ratio" refers to the C/N ratio at the point of maximum N accumulation (McClaugherty et al. 1985). After this point is reached the litter starts to release N. According to this concept, the critical C/N ratio of woody roots in the Pacific Northwest was from 100 to 180,

**Fig. 8.** Mass and N content of decaying roots at Cascade Head.

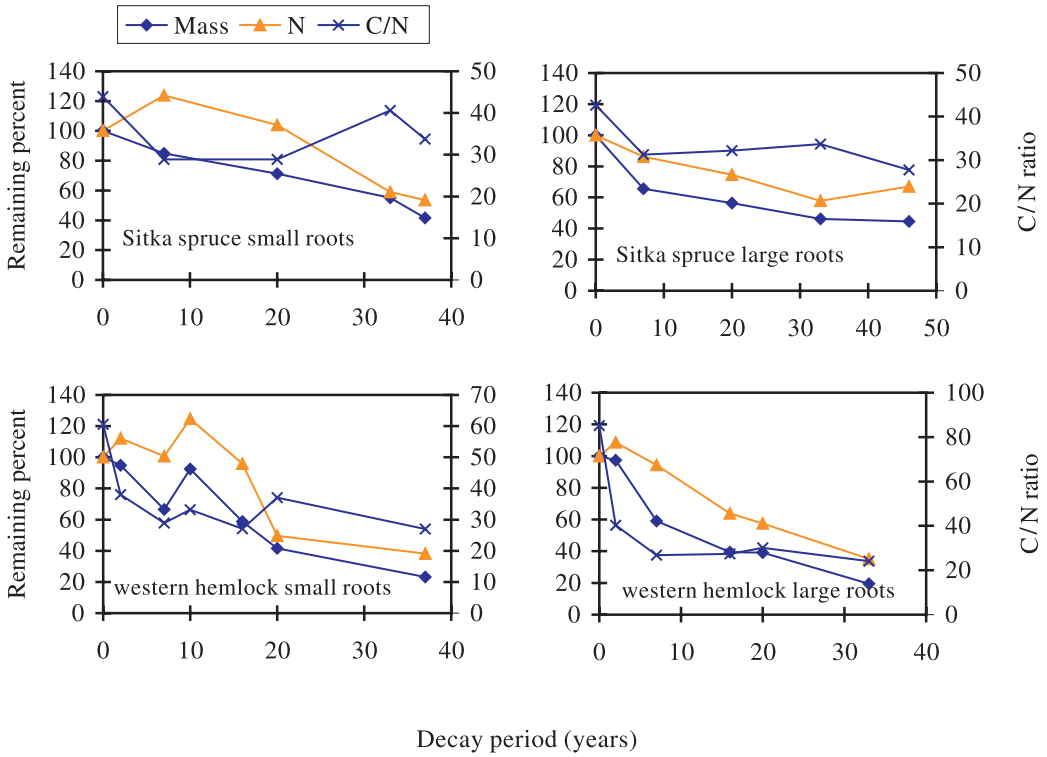
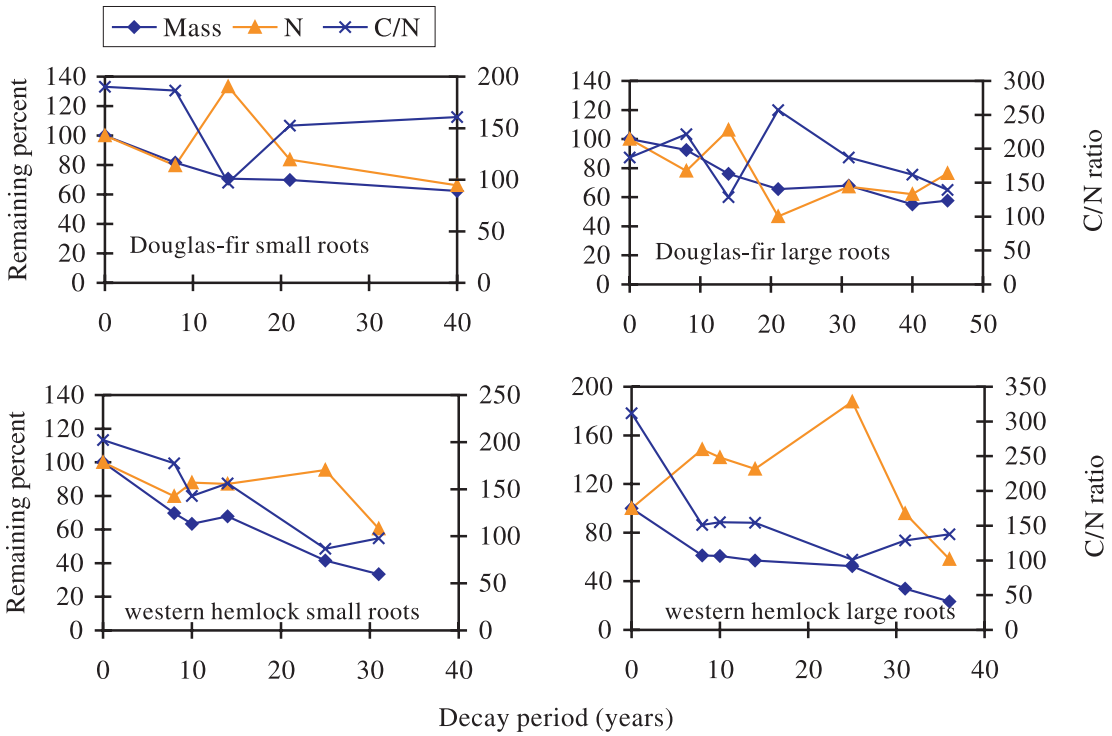
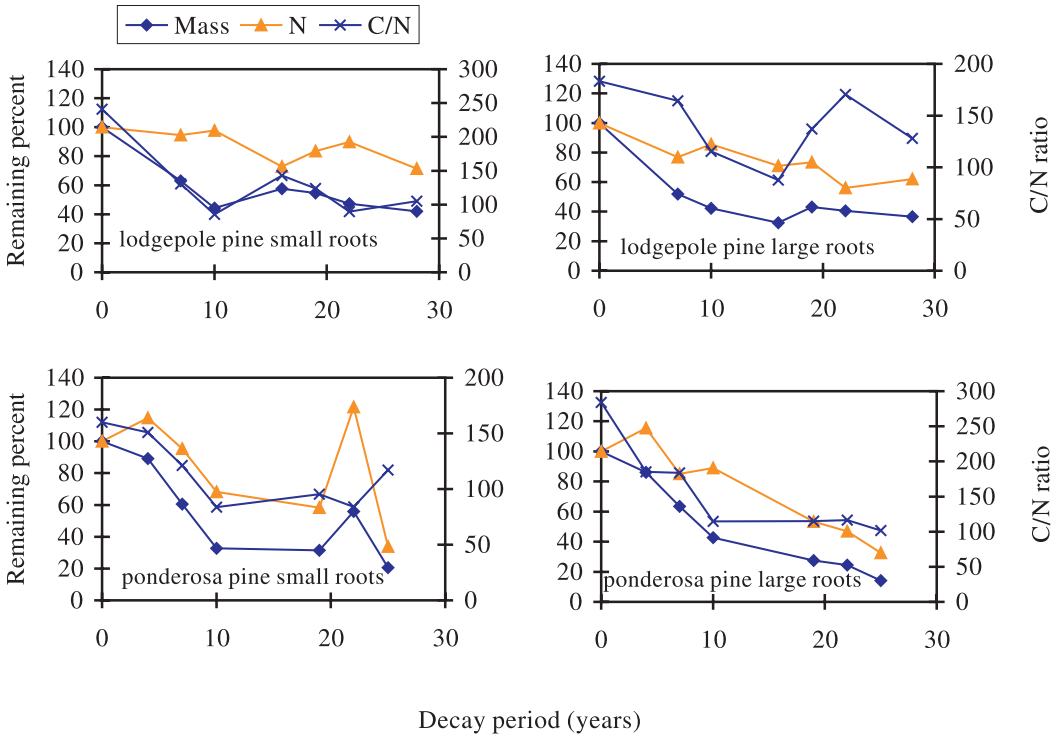



**Fig. 9.** Mass and N content of decaying roots at H.J. Andrews.




at a time when immobilization would have been predicted from published critical C/N ratios. This number was much higher than the critical C/N ratio of other litters. McClaugherty et al. (1985) reported critical ratios of 25 to 45 for the foliage and needle litter of most temperate hardwood forest species, with the highest critical C/N ratio being 70 for red maple (*Acer rubrum* L.) wood. One reason for the high critical ratio of dead roots may have to do with the nature of their C constituents. Dead woody roots generally contain more recalcitrant C and less labile C than fine roots

**Fig. 10.** Mass and N content of decaying roots at Pringle Falls.




(McClaugherty et al. 1984; Chen 1999) and other fine litter (Melillo et al. 1982; Fogel and Cromack 1977). Most microbes, especially brown rots, prefer energy rich and easily decomposable labile C to recalcitrant organic matter. Therefore labile C in woody roots may be less available than the C in fine litters. This would allow N to be released at a far higher C/N ratio in the former substrate. From this viewpoint, the use of total C in the critical C/N ratio calculation may not be appropriate. Instead, use of labile C of organic matter may be more appropriate than total C.

Nitrogen released from decomposing woody roots may be controlled by factors other than critical C/N ratios. Harmon et al. (1994) reported several N loss pathways including fragmentation, absorption from mycorrhizae and roots, leaching, insects, and fungal sporocarps that remove N from woody detritus. Nitrogen in dead roots could be transported into the adjacent soils by fungal hyphae. Some mycorrhizal seedlings could derive a significant proportion of their N from organic sources such as dead roots (Turnbull et al. 1996). Since bark N concentrations were much higher than those of wood (Chen 1999), fragmentation of bark could also contribute to N loss. Leaching is another possible pathway of N released from decomposing roots, especially at the CAH site with high precipitation.

### Management implications

Decomposition of woody roots in coniferous forest ecosystems in the Pacific Northwest has management implications for soil strength, belowground habitat, and nutrient dynamics. Woody roots influence soil strength, but the mechanical reinforcement provided by living roots diminishes after they die and start to decompose. The occurrence of decay-resistant resin cores in some species may offset this trend. Although soil erosion and landslides are also controlled by geologic and climatic factors (Swanson et al. 1987), our data may help predicting soil erosion and landslides in the Pacific Northwest. Because of the slow decomposition of root bark, it is common to find many hollow dead roots in forest soils. These belowground channels may provide habitats for animals, including a variety of salamanders (such as the clouded salamander, ensatina, and western redback salamanders), shrews (e.g., the Troubridge's shrews), the shrew-mole, the coast mole, the western red-backed vole, and Townsend's chipmunk (J. Hayes, personal communication). Nitrogen release from dead woody roots may have implications for tree nutrition. In the Pacific Northwest, harvests may create up to 200 Mg/ha of dead roots (Vogt et al. 1986). Our results suggest that after 4–7 years of decomposition, the release of N from this mass of dead roots matches the demand of a rapidly regenerating forest. This synchrony between N release and tree regeneration may have important implications for the sustainable development of forest ecosystems in the Pacific Northwest and therefore bears additional examination.

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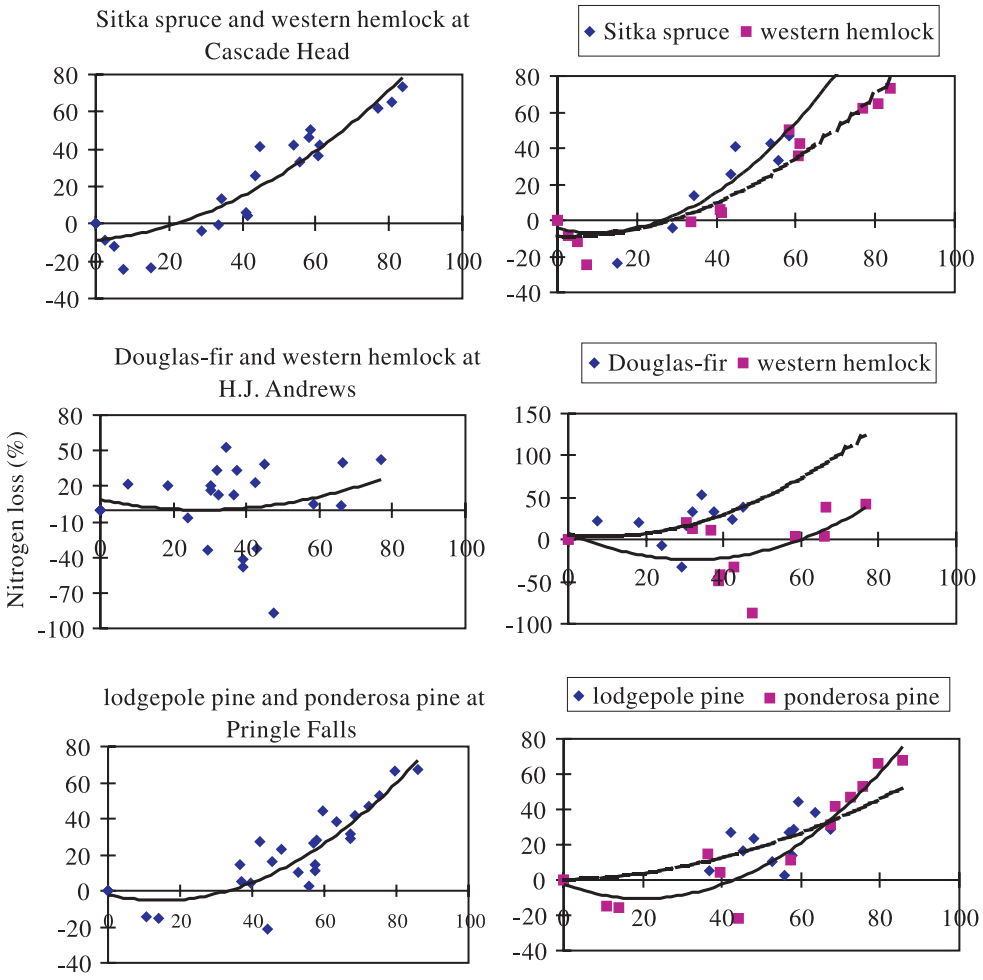
**Fig. 11.** Nitrogen content of roots as a function of mass loss at three sites.

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