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Title: ROOT DECOMPOSITION IN THREE CONIFEROUS FORESTS: EFFECTS OF SUBSTRATE QUALITY, TEMPERATURE, AND MOISTURE.

Abstract Approved: Signature redacted for privacy.

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Controls of substrate quality, temperature, and moisture on woody root decomposition in the Pacific Northwest were explored using chronosequences, time series, laboratory incubations, and simulation modeling approaches at three sites: Cascade Head (CAH), H. J. Andrews (HJA), and Pringle Falls Experimental Forests (PRF).

In the chronosequence study, a structural component-oriented approach provided a better estimation of long-term mass loss than initial substrate indices. Western hemlock and ponderosa pine had higher decomposition rate-constants (k = 0.033 to 0.077/year) than Sitka spruce, Douglas-fir, and lodgepole pine (k = 0.011 to 0.03/year). This was mainly due to the presence of root resin cores in the latter species. During the first 2-years of decomposition in a time series experiment, species significantly affected mass loss in fine and small roots (< 1 cm), but not in larger sized roots. No significant difference among sites were observed. Woody root decomposition decreased with increasing root size. Lignin:N and phenols:N ratios were good predictors of k for fine and small roots, respectively, although none of 17 initial substrate indices was a good predictor of k of larger roots. In both chronosequence and time series decomposition studies, dead roots released nitrogen in the early stages of decomposition.

In laboratory incubations, dead root respiration was optimum at 30-40 °C. The Q_{10} of root decomposition was influenced significantly ($P < 0.01$) by incubation temperature range, but not by species, decay class or the direction of temperature change. Dead root respiration reached an optimum when moisture content was between 100 and 275%. Exchange of moisture between roots and soils appeared to follow a diffusion process, with larger roots equilibrating more slowly than smaller roots.

A model, ROOTDK, captured the overall mass loss pattern of Sitka spruce, Douglas-fir, and western hemlock but not of lodgepole pine and ponderosa pine. Root decomposition at CAH and PRF is more sensitive to climatic changes than HJA. Thus, even within the Pacific Northwest region the response of root decomposition to an altered climate can be divergent.

Root Decomposition in Three Coniferous Forests: Effects of Substrate Quality, Temperature, and Moisture

by

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CONTRIBUTION OF AUTHORS

Dr. Mark E. Harmon was involved in the design, analysis, and writing of each manuscript. The laboratory incubation study was conducted in the laboratory of Dr. Robert P. Griffiths who also assisted in the interpretation of data. Dr. Steve Garman was involved in the data analysis of modeling manuscript. Mr. Jay Sexton helped to collect data for time series study.

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ROOT DECOMPOSITION IN THREE CONIFEROUS FORESTS: EFFECTS OF SUBSTRATE QUALITY, TEMPERATURE, AND MOISTURE

CHAPTER 1

INTRODUCTION

1.1 INTRODUCTION

Roots are important structural and functional components of forested ecosystems (Grier et al., 1981; Harris et al., 1977, 1980; Hermann, 1977). Roots not only serve to anchor plants in soil physically, but also absorb water and nutrients from soil for plants. A large amount of forest production is allocated to roots, similar in magnitude to foliage production, resulting in a large flux of carbon and nutrients into the belowground system (Harris et al., 1977; Kurz et al., 1996; McClaugherty et al., 1982; Persson, 1979, 1980; Vogt et al., 1986). Although root systems store large amounts of organic matter and nutrients in forest ecosystems, past studies on root dynamics have primarily focused on production and growth (Cairns et al., 1997; Grier et al., 1981; McClaugherty et al., 1982; Persson, 1979, 1980; Santantonio, 1982). The few root decomposition studies that have been conducted were carried out on fine roots in young forest stands and were short-term (i.e., usually 1 year) (Camire et al., 1991). Information on the rates and controls of root decomposition is scant, especially compared to the wealth of aboveground litter decomposition data (Berg, 1984; Harmon et al., 1986; Vogt et al., 1986; Waid, 1974). More root decomposition studies are needed.

Decomposition of woody roots, like fine litters, is profoundly influenced by litter substrate quality, the decomposer community (biotic factors), and climatic environment (abiotic factors) (Heal et al., 1997; Swift et al., 1979). The relative importance of biotic and abiotic factors and how these interact, however, is poorly understood. The major biotic factors that may affect root decomposition include nitrogen, lignin, and carbon concentration of roots, proportions of bark and wood, decomposer

organisms present, and their colonization patterns. Initial lignin : nitrogen ratio has been regarded one of the best biotic predictors of root decomposition (Berg, 1984; Camire et al., 1991; Fogel and Cromack, 1977; McClaugherty et al., 1984, 1985). Abiotic factors with the potential to influence root decomposition include temperature, moisture, oxygen concentration, and soil properties such as texture and nitrogen availability. Of these, temperature and moisture content are regarded as the main abiotic factors influencing root decomposition (Santantonio and Grace, 1987). Isolating the temperature and moisture effects on decomposition from biotic factors is increasingly important if we are to understand the impact of climate change (Anderson, 1992).

1.2 AVAILABLE METHODS

Given that root decomposition is an important process, how does one measure it? Chronosequences, time series, and laboratory incubations are three major methods to determine the rate and effects of controls on the decomposition of litter. Each method has advantages as well as disadvantages. The chronosequence method involves determining the length of time logs, branches, or roots have been dead and how density, volume, or other characteristics of interests change over time using a substitution of space for time (Yavitt and Fahey, 1982, Harmon et al., 1986). This method can provide a general long-term pattern of decomposition in short-term study period, but uncertainties about initial conditions, time since death, and environmental differences exist (Harmon et al., 1990). In contrast, time series experiments control the initial conditions of samples, the time of death, and one can better control environmental differences. Thus they provide more accurate decomposition data than the chronosequence method does. Moreover, the time series approach is more amenable to reciprocal transplant experimental studies that test biotic versus abiotic controls. However, this method generally takes years or decades to complete the experiment. Laboratory incubations allow controlled experiments that test the effects of abiotic factors (e.g., temperature, moisture) and selected organisms (Heal et al., 1997; Taylor and Parkinson, 1988) in a short-term study period. Thus this approach is able to isolate the temperature and moisture effects on decomposition from other controls,

information that is very difficult to achieve in field studies. The main purpose for laboratory incubation studies is to understand how the change of controls such as temperature, moisture, and substrate quality influence decomposition in relative sense, but not to measure the absolute rate of long-term decomposition. Thus chronosequences, time series, and laboratory incubations are complementary approaches. To better understand the controls of substrate quality, temperature, and moisture content on woody root decomposition, I have used each of them in this study.

1.3 OBJECTIVES

The overall goal of this study was to understand how substrate quality, temperature, and moisture content control root decomposition and nitrogen release in the Pacific Northwest. To do this, I examined these processes at three sites across an environmental gradient in Oregon: Cascade Head Experimental Forest (CAH), H. J. Andrews Experimental Forest (HJA), and Pringle Falls Experimental Forest (PRF). Five dominant species Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*) were used in this root decomposition study. Four key sets of questions were addressed.

1. How do the decomposition rate-constants of woody roots vary with species and/or size? Do the decomposition rate-constants of woody roots decrease with increasing root size for the same species?

2. How do the initial structural components (e.g., bark, wood, and resin core proportions) and substrate quality indices (e.g., lignin: N ratio, C: N ratio) of woody roots influence root decomposition? Can the decomposition rate-constants of woody roots be predicted from initial structural components or substrate quality index or both?

3. How do the decomposition rate-constants of woody roots vary with sites differing in thermal-moisture conditions? How do soil temperature and moisture influence woody root decomposition?

4. How will climate changes potentially influence root decomposition at the three sites examined? Which sites are more sensitive to changed climate in root decomposition?

1.4 CHAPTER ARRANGEMENT

To answer these questions I used a variety of methods: chronosequences, time series, laboratory incubations, and simulation modeling. Factors controlling woody root decomposition of Sitka spruce, Douglas-fir, western hemlock, ponderosa pine, and lodgepole pine are studied by the chronosequence method in **Chapter 2**. Questions 1 and 2 were examined by sampling chronosequences of dead roots created by timber harvests at CAH, HJA, and PRF. This allowed me to compare the decomposition rate-constants of root structural components and whole roots and to test the degree structural components, species, size, substrate quality, and climate controlled root decomposition. Finally the long-term dynamics of carbon and nitrogen of decomposing roots were examined.

To further gain more temporal resolution on the processes examined in Chapter 2, a long-term (10 years) root decomposition time series study with a split-split plot experimental design was established using litterbag techniques. This allowed me to examine questions 1-3 in more detail. This experiment was designed to test the effects of species, root size, and sites on root decomposition at the CAH, HJA, and PRF sites. The split-plot experimental design included 4 plots within each site, 5 size classes, and 4 "backbone" species. The 5 size classes included fine roots (< 2 mm diameter), small roots (2-10 mm), medium roots (10-50 mm), large roots (50-100 mm), and jumbo roots (> 100 mm). The "backbone" species were red alder (*Alnus rubra*), Douglas-fir, western hemlock, and ponderosa pine. In addition, another 11 fine root species, 4 small roots, and 3 medium roots species were included in the study. A total of 4500 root bags were buried at the 12 plots for a 10 year study. In **Chapter 3**, the first 2.5 year results of root decomposition are reported.

Although the chronosequences and time series studies demonstrated substrate quality and site effects on root decomposition, the natural covariance between

temperature and moisture in field studies makes it difficult to disentangle the individual effects of temperature and moisture. Therefore a laboratory incubation study in which temperature and moisture regimes could be manipulated was carried out to answer question 3. **Chapter 4** reports the results of temperature, moisture, and their interaction on respiration of five species from the three field sites.

Moisture dynamics of dead roots in soils have not well studied, although a strong relationship between woody root moisture and soil moisture is assumed in many models. In **Chapter 5**, I report a preliminary laboratory study that explores how species, root size, and soil moisture influence moisture dynamics of dead roots. Two simple experiments representing two extreme conditions were conducted. In the first, water saturated roots were placed in dry soils. In the second, dry roots were buried in very wet soils. A simple diffusion model with two parameters was used to fit changes of root moisture of both experiments.

Results from the chronosequences, time series, laboratory incubations, and soil-root moisture dynamic studies were synthesized into a simulation model -- ROOTDK. In **Chapter 6,** I describe the model, perform a sensitivity analysis, evaluate the model performance, and use the model to explore the implications of climate change on root decomposition in the Pacific Northwest. Root decomposition of five species from the three sites were simulated under current climate. Four climate change scenarios were then used to test the impacts of changed climate on Douglas-fir root decomposition at the CAH, HJA, and PRF sites. These four climate change scenarios were increased temperature but unchanged moisture (ITUM), increased temperature and decreased moisture (ITDM), unchanged temperature and increased moisture (UTIM), and both increased temperature and moisture (ITIM). In these simulations, soil temperature was increased 3 °C from the seasonally averaged soil temperature of each site. For the moisture change scenarios moisture contents were decreased or increased by 10% from current seasonally averaged soil gravimetric moisture at CAH, HJA, and PRF, respectively.

CHAPTER 2

ORGANIC MATTER, CARBON, AND NITROGEN DYNAMICS OF DECOMPOSING WOODY ROOTS IN CONIFEROUS FORESTS OF THE PACIFIC NORTHWEST: A CHRONOSEQUENCE APPROACH

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2.1 ABSTRACT

Woody root decomposition was studied in Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*) forests at Cascade Head, H. J. Andrews, and Pringle Fall Experimental Forests in Oregon, using a chronosequence approach. Root samples of five species were excavated from stumps whose ages ranged from 0 to 46 years old. Root wood showed the fastest decomposition rate-constants (k), root bark the second, and resin cores the slowest. In order of increasing k the species were: Douglas-fir < Sitka spruce < lodgepole pine < western hemlock < ponderosa pine. The occurrence of resin cores in woody roots of Douglas-fir, Sitka spruce, and lodgepole pine greatly slowed the decomposition of whole roots for these species. Our study indicated a structural component-oriented approach of woody root decomposition provided a better estimation of long-term mass loss than initial substrate quality indices. None of the 13 initial substrate quality indices was a good predictor of root decomposition. The substrate quality of woody roots therefore corresponded more to physical structures than chemical indices. A double-exponential model fit better than a single-exponential model for decomposing woody roots with resin cores. Root size did not appear to influence root decomposition for the five species examined. The effect of climate on root decomposition was apparently overridden by differences in species. Rot types in dead roots varied with species. White-rots occurred frequently in ponderosa pine and lodgepole pine, whereas brown-rots mostly appeared in Douglas-fir and Sitka spruce. Decomposing woody roots started to release nitrogen after 20-30% mass loss, a point when the C:N ratio of dead roots averaged 140. Nitrogen in woody roots was released slower than mass or carbon. However, this element was released at a time when immobilization would have been predicted from published critical C:N ratios.

2.2 INTRODUCTION

Roots are important structural and functional components of forested ecosystems (Grier et al., 1981; Harris et al., 1977, 1980; Hermann, 1977). Roots not only serve to anchor plants in the soil physically, but also absorb water and nutrients

from soil for plants. To maintain these functions, a large amount of forest production is allocated to roots, similar in magnitude to foliar production (Harris et al., 1977; McClaugherty and Aber, 1982; Persson, 1979, 1980). This results in a large flux of carbon and nutrients into the belowground system (Cairns et al., 1997; Kurz et al., 1996; Vogt et al., 1986). In coniferous forests, root biomass is an especially large fraction of total stand biomass, total stand annual production, and total input of organic matter to the soil (Nadelhoffer and Raich, 1992; Vogt et al., 1991). Yet few studies have directly examined the roles of dead roots in carbon and nutrient cycling of forest ecosystems (Heal et al., 1997).

Belowground processes represent a significant constraint to forest ecosystem responses to global climate change. Living and dead roots, the most important components in the belowground system, have been increasingly recognized in soil-mediated responses of forest ecosystems to global climate change (Curtis et al., 1994). The nature and magnitude of these responses are controlled, to a great extent, by the dynamics of root production, and growth, as well as decomposition (Norby, 1994). Of these processes, root decomposition is important in controlling root responses to global climate change (Norby, 1994). Root decomposition data of various forest ecosystems is extremely scant compared to aboveground litter decomposition.

Despite this increased awareness of the importance of root decomposition, this process, especially for woody roots and their related carbon and nitrogen dynamics, has not been studied frequently, in part because of the general technical difficulty in studying belowground processes (Fahey and Arthur, 1994; Fahey et al., 1988; Harmon et al., 1986; Heal et al., 1997; Vogt et al., 1986; Waid, 1974; Yavitt and Fahey, 1982). Those few root decomposition studies that have been conducted have focused on fine root decomposition (Aber et al., 1990; Bloomfield et al., 1993; McClaugherty and Aber, 1982; McClaugherty et al., 1984; Persson, 1980; Santantonio and Grace, 1987). Far less is known about the decomposition, controls of this process, and carbon and nitrogen dynamics of woody roots.

Litter decomposition is profoundly influenced by litter substrate quality, climatic environment, and the decomposer community (Heal et al., 1997; Swift et al., 1979). Of

the various indices of initial substrate quality, lignin:N and C:N ratios seem to be the best predictor of litter decomposition, especially for fine litter (Berg, 1984; Fogel and Cromack, 1977; Hobbie, 1996; Melillo et al., 1982). However, these indices have potential limitations in predicting woody root decomposition. First, different species woody roots do not exhibit the apparent differences in lignin:N and C:N ratios observed in fine litter. That makes it difficult to use them to predict woody root decomposition. Second, the values of these indices are quite different from those of fine litter, going into a range where minimal response is expected. For example, the lignin:N ratio of most woody roots (larger than 2 cm in diameter) is about 100-130, well beyond the 10 to 50 range of fine litter. Moreover, lignin:N ratio is not a good decomposition predictor when the ratio is above 80 (Harmon et al., 1990). Third, the control of substrate litter quality on decomposition changes over time. Berg and Staaf (1980) found the shift from nutrient control in early decomposition stages of *Pinus sylvestris* 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 initial substrate quality indices. Woody roots of various species show apparent differences in root structural components qualitatively and quantitatively. Woody roots are comprised of bark, wood, and in some cases, a resin core analogous to knots in tree boles. These components appear to decompose at different rate-constants. Moreover, the proportions of these structural components vary with species and root sizes suggesting these variations might control their decomposition rates. For example, on a volume basis the fraction of bark ranged from 48% in the small (0.5 - 1.0 cm) roots to 26% in the large (2.6 to 5.0 cm) roots (Yavitt and Fahey, 1982) in lodgepole pine forests in Wyoming. A similar pattern was found at Hubbard Brook Experimental Forests, New Hampshire where bark comprised 18.4 to 70.3% of root biomass, depending on species (Fahey et al., 1988). A structural component-oriented approach examines the decomposition of different components of woody roots separately in order to predict whole root decomposition.

We hypothesized that differences in woody root decomposition rate-constants among species for a particular size class 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 the woody roots without resin cores. Moreover, the woody root decomposition rate-constant should decline with increasing root diameter because of a higher volume:surface area ratio and more time required for fungal colonization of larger diameter roots, and an increasing proportion of resin cores (Fahey et al., 1988; Harmon et al., 1986). Finally we predicted that because of the high initial C:N ratio, decomposing woody roots would initially experience a long nitrogen accumulation period and then release nitrogen gradually during the later decomposition stages.

Our study was aimed to measure how fast the woody roots of five important coniferous species of the Pacific Northwest decomposed, and to understand what controlled this process and the associated carbon and nitrogen dynamics. We sampled chronosequences of dead roots created by timber harvest and thinning to study the decomposition of woody roots at Cascade Head Experimental Forest (CAH), H.J. Andrews Experimental Forest (HJA), and Pringle Falls Experimental Forest (PRF). We compared the decomposition rate-constants of root structural components and whole roots and then tested the degree structural components of species, size, substrate, and climate controled root decomposition. Finally, nitrogen dynamics of decomposing roots were examined to identify the periods of uptake and release.

2.3 STUDY SITES AND METHODS

2.3.1 Study sites

This study was conducted in Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*) dominated forests at CAH, HJA, and PRF, respectively (Figure 2-1). These three sites form a climatic gradient from warm and wet at CAH to cool and dry at PRF site. Two dominant coniferous species were chosen at each site. They were Sitka spruce and western

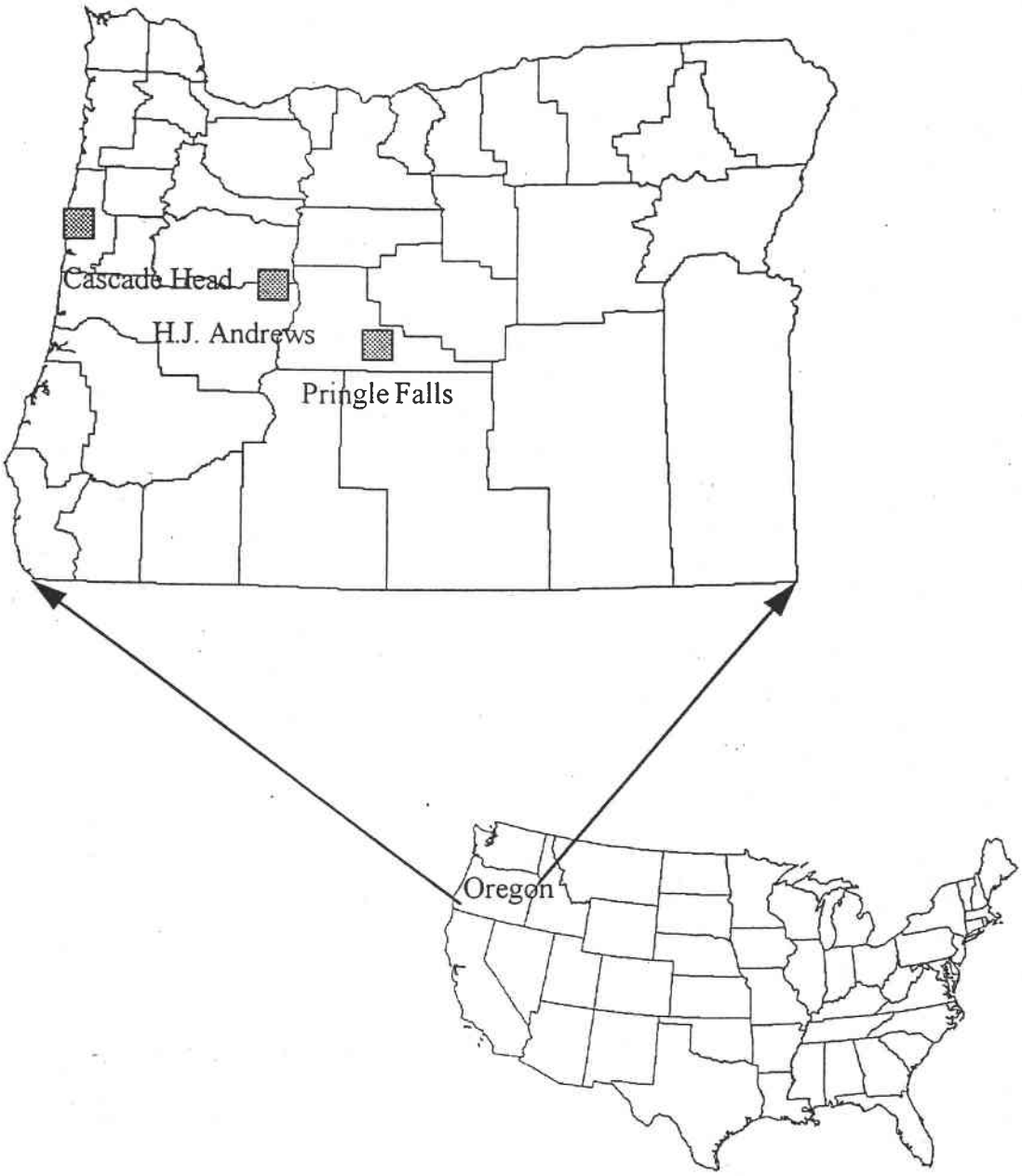

Figure 2-1. Locations of study sites.

hemlock (*Tsuga heterophylla*) at CAH; Douglas-fir and western hemlock at HJA; and ponderosa pine and lodgepole pine (*Pinus contorta*) at PRF.

CAH is located on the Pacific coast near Otis, Oregon. The climate is maritime, with a mean annual temperature of 10 °C and total annual precipitation of 3420 mm. The soils are silt loams to silty clay loams derived from marine siltstones, moderately well drained, and high in organic matter and nitrogen. The dominant forest type is a mixture of western hemlock and Sitka spruce, although small stands dominated by Douglas-fir also occur.

HJA is located 80 km east of 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 typic dystrochrepts; slope gradients range from 20-60%. The forests are classified into two major zones, the western hemlock zone (300-1550 m elevation) and the Pacific silver fir zone (1050-1550 m elevation). Douglas-fir and western red cedar (*Thuja plicata*) are also major components of both zones (Franklin and Dyrness, 1973).

PRF is located in 57 km southwest of Bend, Oregon; east of the Cascades. The climate is modified continental, with a mean annual temperature of 5.7 °C and total 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 between 1310 and 1470 m. The forests are dominated by ponderosa pine and lodgepole pine.

2.3.2 Methods

Root selection. Three separate chronosequences of commercially thinned and clear-cut harvest sites were located at CAH, HJA, and PRF sites. Current stand vigor and locations, as well as thinning or cutting ages, were considered during stand selection. Vigorous forest stands indicated, to some degree, the previous stands were healthy and the chance of root-rot was small. All sampled stands were close to each other and similar in elevation, topography and soil type. At CAH, the chronosequences

included 7 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 ago. Root samples of western hemlock were obtained from trees cut 2, 7, 10, 16, 20, 33, and 37 years prior to sampling (Table 2-1). The second chronosequence, located in the western hemlock zone (300-1550 m elevation) at HJA, included 8 different ages spanning 8 to 45 years after cutting. Douglas-fir occurred in 8 and western hemlock occurred in 7 of these stands. The third chronosequence was located at PRF where ponderosa pine roots were sampled 6 stands which ranged in age from 4 to 25 years. Lodgepole pine roots were sampled in the same stands except for the 4 year-old stand where it did not occur (Table 2-1). Samples of undecayed woody roots from fresh uprooted trees of these species were sampled to serve as "controls".

Woody root decomposition. Decomposition of woody roots was estimated from changes in ash free density of root components. Five stumps were selected for each species at each stand. We avoided "living" stumps to reduce the time lag between when the tree was cut and when the roots died. 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. 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 excavating the soil surrounding roots, 10-20 cm long samples were removed using a handsaw, reciprocating saw, or in the case of very large roots a chainsaw. 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 decomposing 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.

Table 2-1. Plots used for root excavation at three sites in the Pacific Northwest.

Site	Species	Plot	Harvested year	Time since death (yrs)
Cascade head	Sitka spruce	1996A	1996	0
	(*Picea sitchensis*)	1989A	1989	7
		1976A	1976	20
		1963A	1963	33
		1959A	1959	37
		1950A	1950	46
Cascade head	western hemlock	1996A	1996	0
	(*Tsuga heterophylla*)	1994A	1994	2
		1989A	1989	7
		1986A	1986	10
		1980A	1980	16
		1976A	1976	20
		1963A	1963	33
		1959A	1959	37
H.J. Andrews	Douglas-fir	1995A	1995	0
	(*Pseudotsuga menziesii*)	NWS6	1987	8
		L116	1985	10
		L523/B130	1981	14
		WS6	1974	21
		B130	1964	31
		B132	1959	36
		L341	1955	40
		L103	1950	45
H.J. Andrews	western hemlock	1995A	1995	0
	(*Tsuga heterophylla*)	NWS6	1987	8
		L116	1985	10
		L523/B130	1981	14
		L704A	1970	25
		B130	1964	31
		B132	1959	36
Pringle Falls	lodgepole pine	1995A	1995	0
	(*Pinus contorta*)	1988A	1988	7
		1985A	1985	10
		1979A	1979	16
		1976A	1976	19
		1973A	1973	22
		1967A	1967	28
Pringle Falls	ponderosa pine	1995A	1995	0
	(*Pinus ponderosa*)	1991A	1991	4
		1988A	1988	7
		1985A	1985	10
		1976A	1976	19
		1973A	1973	22
		1970A	1970	25

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

$$V = \pi * (D^2 * L)/(4)$$

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's volume. Finally, the presence of brown- *vs.* white-rots associated with the decomposing wood of roots was visually evaluated and recorded in the field. Brown-rots attack primarily the cellulose of cell walls, leaving behind a network consisting of modified lignin. The affected wood develops a brown color. White-rot fungi degrade both lignin and cellulose, leaving behind a spongy or stringy mass. The affected wood 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 returned to the laboratory and were dried to a constant mass at 65 °C and weighed. Densities of bark, wood, and resin cores of each individual root sample were calculated as the oven dry weight 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. 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, nitrogen, and organic constituents.

Soil nitrogen availability. The ion exchange resin bag method has proved a simple measure of in-site patterns of nitrogen availability that is relevant to ecosystem nutrient cycling and production (Binkley, 1984; Binkeley and Matson, 1983). Soil nitrogen availability of the three sites was therefore measured by ion exchange resin bags (Binkley, 1984; Binkley and Matson, 1983). Resin bags were prepared by placing mixed-bed ion-exchange resin (J. T. Baker catalog no. 4631-1) in nylon stockings (Binkley and Matson, 1983). Each bag contained 30 g moist weight of resin (equivalent to about 16.5 g dry weight) with anion and cation exchange capacities of

2.6 meq/g. We selected four stands at each site and buried 10 resin bags which were connected by a nylon line in the top 20 cm soil at each stand in the June of 1995. These resin bags were collected one year later and air dried. Finally, we analyzed ammonium and nitrate concentrations of each resin sample. Four to 5 g dry resin of each resin sample was extracted with 50 ml of 1 M KCI. Ammonium and nitrate were determined by automated solution chemistry procedures (McClaugherty et al., 1985). Extracts of resin blanks had no detectable ammonium or nitrate. Soil nitrogen availability was expressed by index of ammonium, nitrate or their summation.

Near Infrared Reflectance Spectroscopy (NIRS). All the samples were scanned using a NIRS (Near Infrared Reflectance Spectroscopy) Systems 6500 analyzer to predict ash and nitrogen concentrations. Calibration is required to known chemical concentrations from laboratory analyses. The NIRS ash calibration was conducted separately for each site, because the amount of decomposition was highly variable among them. About 38-46% (135, 200, and 167) of the root samples were randomly selected out of a total 352, 439, and 407 root samples for CAH, HJA, and PRF sites, respectively, for ash content calibration. The sample set of nitrogen calibration was randomly selected on the whole root sample set. About 14% (168) of root samples was selected from 1198 samples for nitrogen calibration analyses (see below). The equations developed from these calibrations were used to predict ash and nitrogen concentration of bark, wood, and resin core samples that had been scanned. Carbon and nitrogen concentration of whole roots were calculated using the concentrations of components and fractions of components. All the density, carbon, and nitrogen values reported in this paper are ash-free values.

Wet chemistry analyses. We analyzed ash, carbon and nitrogen concentrations of the selected root samples at Soils Laboratory of Forest Science, Oregon State University. Ash content was determined by heating in a muffle furnace at 500 °C for 4 hours. The total organic carbon of most samples was approximately estimated from ash data (Allen et al., 1974), although the organic carbon of 48 root samples was measured using Carlo-Erba C-N analyzer (NA 1500). Comparing with the organic carbon data from C-N analyzer, we found the ash-based method

underestimated organic carbon concentration slightly. The organic carbon formula can be expressed as follows.

Carbon % = (100-ash%)/Conversion factor

where the conversion factor was obtained from the C-N analyzer. The conversion factor for decomposing root bark and root wood was 1.87 (se = 0.16, n = 24) and 1.93 (se = 0.18, n = 24) respectively while the factor of whole roots was 1.90 (se = 0.17, n = 48).

Nitrogen was measured either by the micro-Kjeldahl technique, with the digestate analyzed by automated solution chemistry procedures (Alpkem Rapid Flow Analyzer 300 series) (McClaugherty et al., 1985), or by Carlo-Erba C-N analyzer. Cross-laboratory comparisons have shown that these two techniques are equivalent (Glassman, personal communication 1997; McLellan et al., 1991a). In this study, nitrogen concentration of 121 root samples was analyzed by Kjeldahl technique and 47 root samples were measured by Carlo-Erba C-N analyzer.

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 extratant (TAPPI, 1975), hot water-soluble polyphenol (Folin-Denis method, Allen et al., 1974), hot water-soluble simple sugars (phenol-sulfuric acid assay, DuBois et al., 1956), acid-soluble carbohydrates (cellulose, hemicellulose, and starch, hydrolysis followed by the phenol-sulfuric acid assay, DuBois et al., 1956), and acid-insoluble carbon (Effland, 1977). Although the acid-insoluble fraction includes other recalcitrant carbon 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.

2.3.3 Statistical analysis

Decomposition rate-constants of root components and whole roots. The most commonly used model in root decomposition studies has been the single-exponential model (Bloomfield et al., 1993; Yavitt and Fahey, 1982). 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. Decomposition rate-constants for bark, wood, resin cores of roots and whole roots were calculated from the linear regressions of the mean remaining density of the structural component, transformed into natural logarithms (ln), versus time. The slope of these regressions was the decomposition rate-constant.

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

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

where Y_{slow} is the relative density of recalcitrant fraction of roots such as resin cores, Y_{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.

Root component controls on decomposition rate-constants. The samples of bark, wood, and resin core from the same root are not independent of each other. Lack of independence is difficult to correct. This data structure leaves us few powerful and robust statistical tools available to test root tissue controls on decomposition rate-constants. In our study, we compared the confidence intervals of the estimated decomposition rate-constant (Jongman et al., 1995). There is a fairly close, but not exact, relationship between the overlap in the confidence intervals and the significance of a test of equal means.

Controls of species and initial root substrate quality on decomposition rate-constants of whole roots. A simple linear regression was developed with decomposition rate-constants as the dependent variable and species or the initial root quality index as independent variables. Species or substrate quality controls on decomposition rate were evaluated based on the *P* value of regression. Furthermore, differences among the decomposition rate-constants of five species examined were

detected by comparing the confidence intervals of decomposition rate-constants (P = 0.05). Due to the unavailability of initial root quality data of Sitka spruce and Western hemlock at CAH, four species were used in this analysis. Each model had 8 observations (4 species X 2 root size classes). Indices of root quality in this analyses included initial concentrations of all the organic fractions as well as N, C, C:N, and lignin:N.

Soil nitrogen availability and decomposition rate-constants of roots. One-way analysis of variance (ANOVA) was used to compare site differences in terms of soil nitrogen availability. Differences between means were detected using Fisher's Protected Least Significant Difference (LSD). Finally, decomposition rate-constants of roots were regressed against the soil nitrogen availability index to examine its effects on decomposition rate-constants of different woody roots.

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 $P \leq 0.01$.

2.4 RESULTS

2.4.1 NIRS prediction of ash and nitrogen concentrations

The calibration equations were based upon samples with a wide range of ash and nitrogen concentrations (Table 2-2), reflecting the diverse sample types and widespread decomposition ages of our root samples. The determination coefficients (R^2) of ash of decomposition root samples ranged from 0.94 to 0.95 (P = 0.0001) (Table 2-3). The standard error of calibration (SEC) and standard error of cross validation (SECV) were low compared to the mean values of ash and nitrogen except for ash of the PRF samples (Table 2-2 and Table 2-3). The calibration results of ash concentration were not as good as reported previously (Joffre et al., 1992). Joffre et al. (1992) obtained a R^2 of 0.99 in ash concentration of leaf litter in a more homogeneous sample set in which the longest decomposition age was only 26 months.

Table 2-2. Range of wet chemical variables used within the NIRS calibration sample set*.

Variable	Site	n	Mean (%)	Range (%)	SE (%)
Ash	Cascade Head	135	3.83	0.11--30.42	4.69
Ash	H. J. Andrews	200	8.27	0.21--55.51	9.76
Ash	Pringle Falls	167	10.52	0.17--69.76	13.42
Nitrogen	Three sites	168	0.46	0.06--1.42	0.24

* n, sample number. SE, standard error.

Table 2-3. NIRS equation calibration statistics for ash and nitrogen of woody roots*.

Variable	Site	n	R^2	SEC (%)	SECV (%)	Calibration Method	Math Treatment
Ash	Cascade Head	135	0.95	0.81	1.70	MPLS	2, 5, 5, 1
Ash	H. J. Andrews	200	0.95	1.35	2.96	PLS	2, 6, 4, 1
Ash	Pringle Falls	167	0.94	2.65	4.99	MPLS	2, 5, 5, 1
Nitrogen	Three sites	168	0.90	0.07	0.13	MPLS	2, 5, 5, 1

* n, sample number.
SEC, standard error of calibration.
PLS, partial least squares.
R^2, Coefficient of Determination.
SECV, standard error of cross validation.
MPLS, modified PLS.

The determination coefficient of nitrogen calibration of root samples was 0.90 (P = 0.001), also lower than some previous studies (Bolster et al., 1996; Joffre et al., 1992; Mclellan et al., 1991a, 1991b; Wessman et al., 1988; Winch and Major, 1981). However, the SEC and SECV, 0.068% and 0.126%, were small compared to the mean nitrogen concentration of root samples, indicating an acceptable nitrogen prediction. In our study, the calibration sample set was highly heterogeneous. For example, the roots samples at HJA included not only different decomposition ages ranging from 0 to 45 years, but also different root components such as bark, wood, and resin cores.

Generally, the predictive accuracy of ash and nitrogen was acceptable, especially considering the heterogeneity of our root samples. Graphic comparisons between values predicted with NIRS calibration equations and those obtained by wet chemical analyses (Figure 2-2) indicated NIRS could successfully determine ash and nitrogen of woody roots as well as for foliage litter (Joffre et al., 1992; McLellan et al., 1991a, 1991b; Wessman et al., 1988). The prediction of ash (Figure 2-2a, b, c) was relatively better than nitrogen (Figure 2-2d), however, ash concentration was slightly underestimated, especially as ash concentration increased. This underestimation of ash prediction was consistent at all three sites.

2.4.2 Decomposition of structural components

2.4.2.1 Density changes over time

Density changes were different among the various root components (Figure 2-3). The initial density of bark was slightly higher than root wood, whereas resin cores had the highest initial density among the root components. The rate of mass loss of root wood was faster than root bark, a result consistent with previous studies (Fahey and Arthur, 1994; Fahey et al., 1988). The density of resin cores showed no significant declining trend. 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

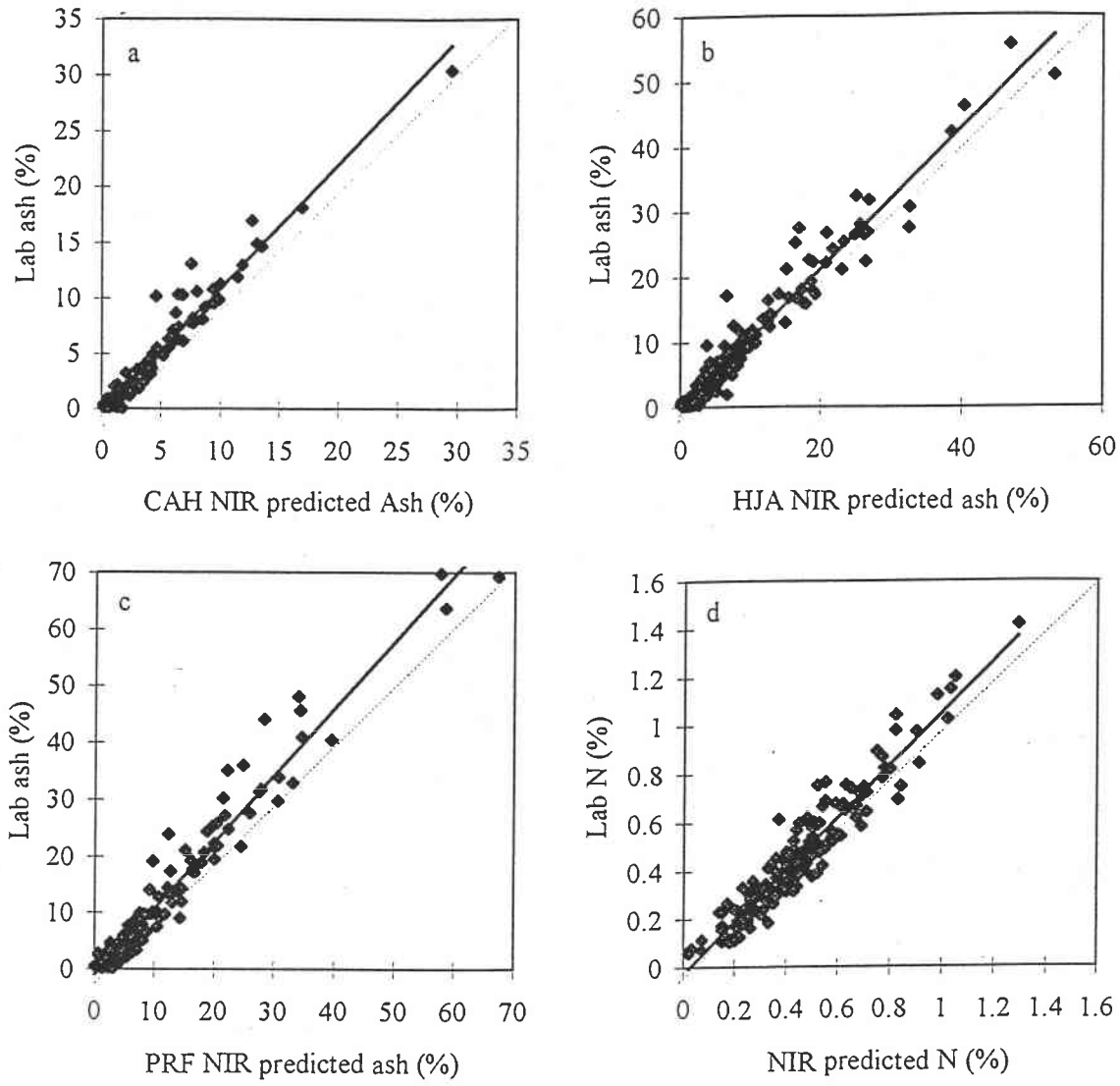

Figure 2-2. Relationship between NIRS predicted values and wet chemistry values (% of dry matter)*.

* Dashed line is a 1:1 line and solid line is a regression line. CAH, HJA, and PRF refer to Cascade Head, H.J. Andrews, and Pringle Falls site, respectively.

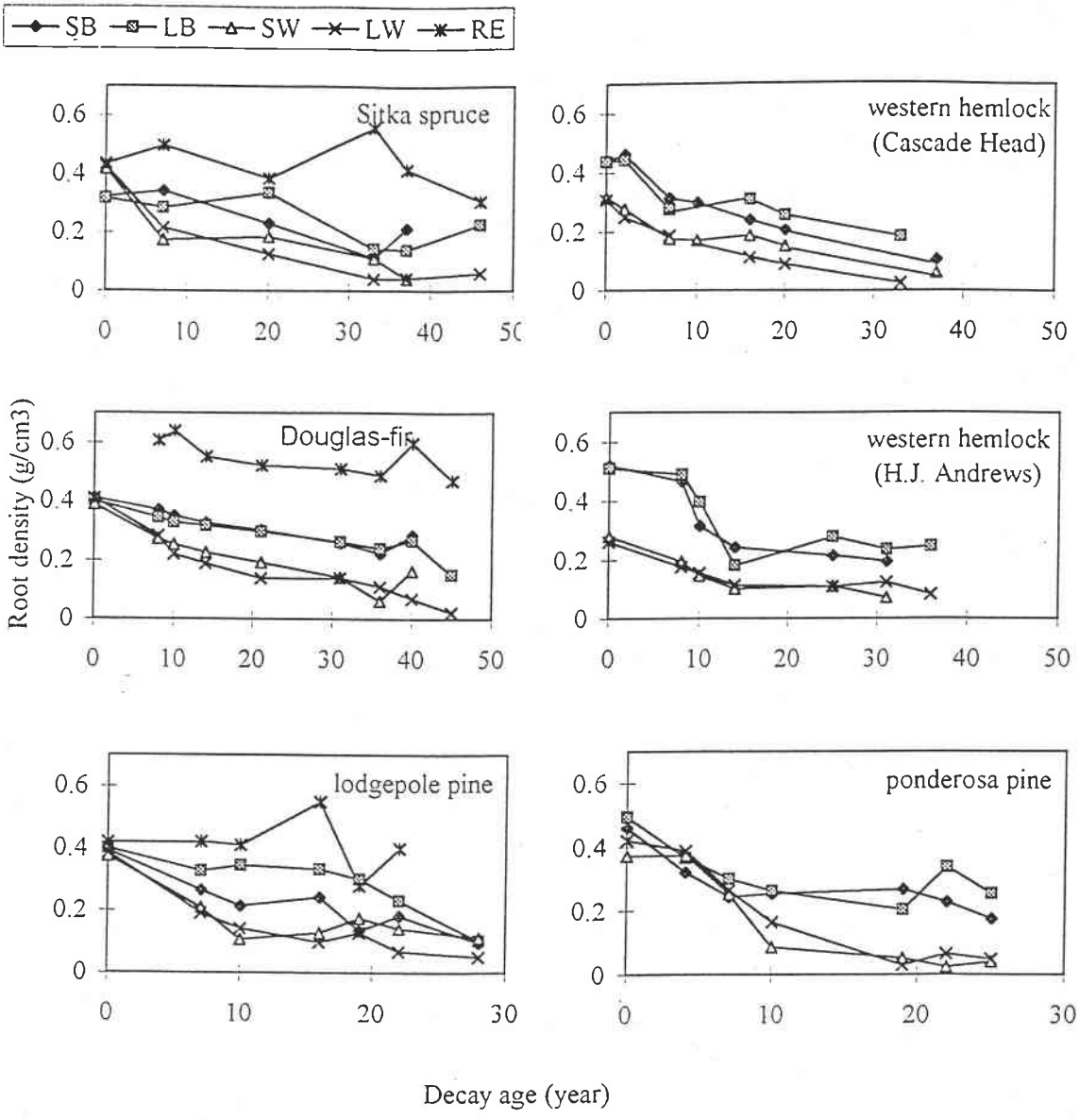

Figure 2-3. Density change of different root components over time.

SB:bark of small roots; BL:bark of large roots; SW:wood of small roots. LW:wood of large roots. RE:resin core.

small roots and large roots. This suggests that root size had little effect on decomposition of either bark or wood.

2.4.2.2 Decomposition rate-constants of root components

Different root components showed clearly different decomposition rate-constants (Table 2-4), with that of wood being the highest ranging from 0.030 to 0.111/year. One exception was for small lodgepole pine roots which had wood rate similar to bark. The decomposition rate-constant of bark was intermediate ranging from 0.011 to 0.044/year, while resin cores showed the lowest rate-constant by an order of magnitude (0.000 to 0.004/year). Comparisons of decomposition rate-constant confidence intervals indicated that the decomposition rate-constants of root wood was significantly higher than that of root bark, especially for ponderosa pine and Douglas-fir (Figure 2-4). The only exception was western hemlock at HJA where the bark and wood decomposition rate-constants did not differ significantly.

When the same root component was compared, species appeared to influence decomposition rate-constant (Figure 2-4). Of the five species examined, the root wood of ponderosa pine showed the highest decomposition rate-constant (0.103 - 0.111/year), although the decomposition rate-constants of root wood in other four species were not statistically different. When comparing small root wood decomposition, Douglas-fir had the slowest rate-constant of 0.030/year. Comparing the root bark decomposition rate-constants among the species, lodgepole pine had fastest bark decomposition rate, ranging from 0.039 to 0.044 /year. In contrast, the bark decomposition rate of Sitka spruce large roots was slowest at only 0.011 /year.

2.4.2.3 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%) (Figure 2-5). 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 occured in

Table 2-4. Coefficients of regressions of single-exponential model used to estimate decomposition rate-constant (k) of root components of dominant coniferous species in the Pacific Northwest.

Site	Species	Component	Diameter (cm)	Regression coefficients[a] Y_0 (g/cm^3)	k (/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
Cascade Head	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
H.J. Andrews	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
Pringle Falls	ponderosa pine	Bark	1--5	0.37	0.026	0.7*	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

[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.
* $0.05 > P > 0.01$; ** $P < 0.01$.

[b] Each data point represents the mean of 4 - 15 samples.

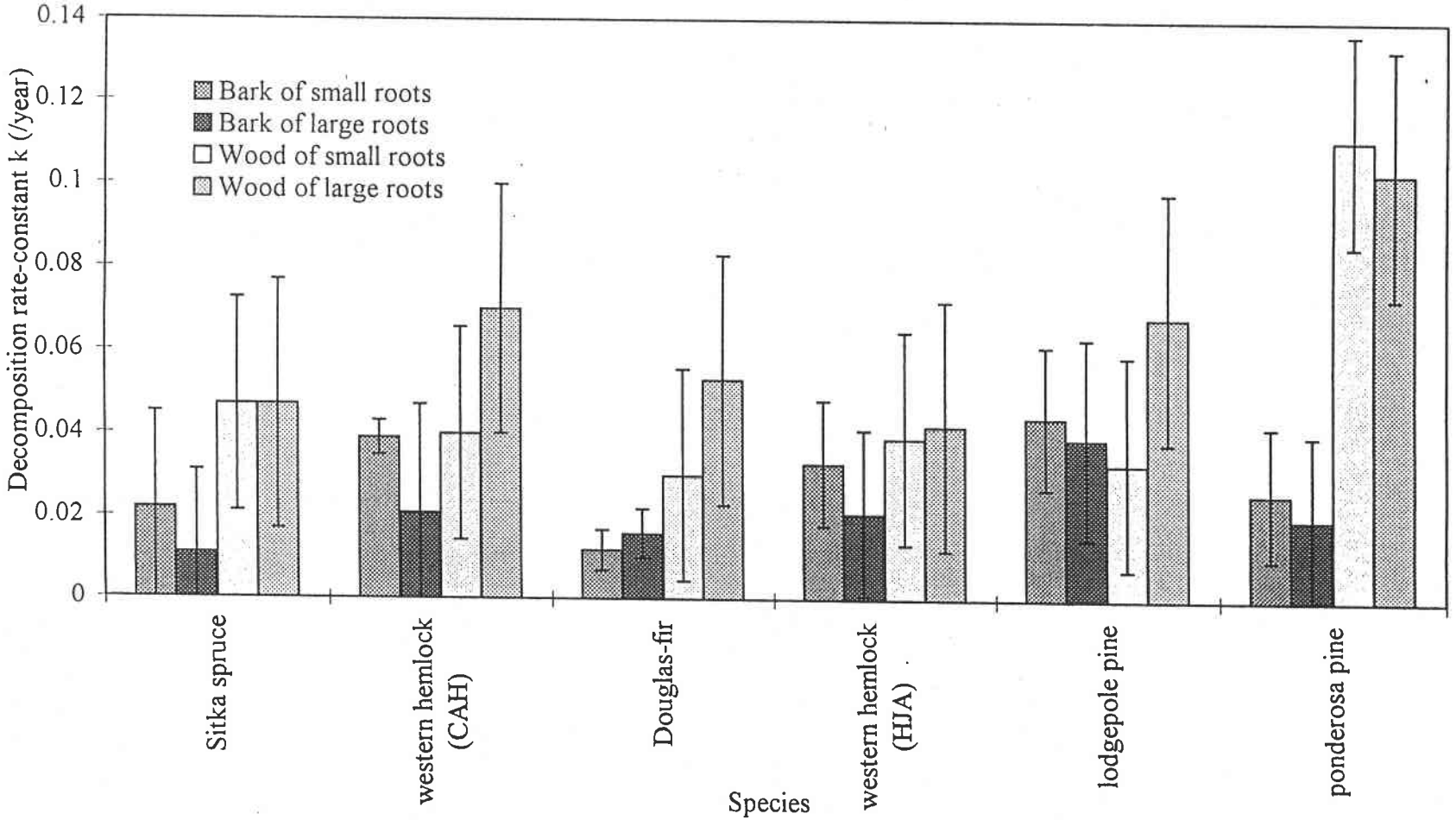

Figure 2-4. Confidence interval of decomposition-rate constant for bark and wood of decomposing roots at three sites.

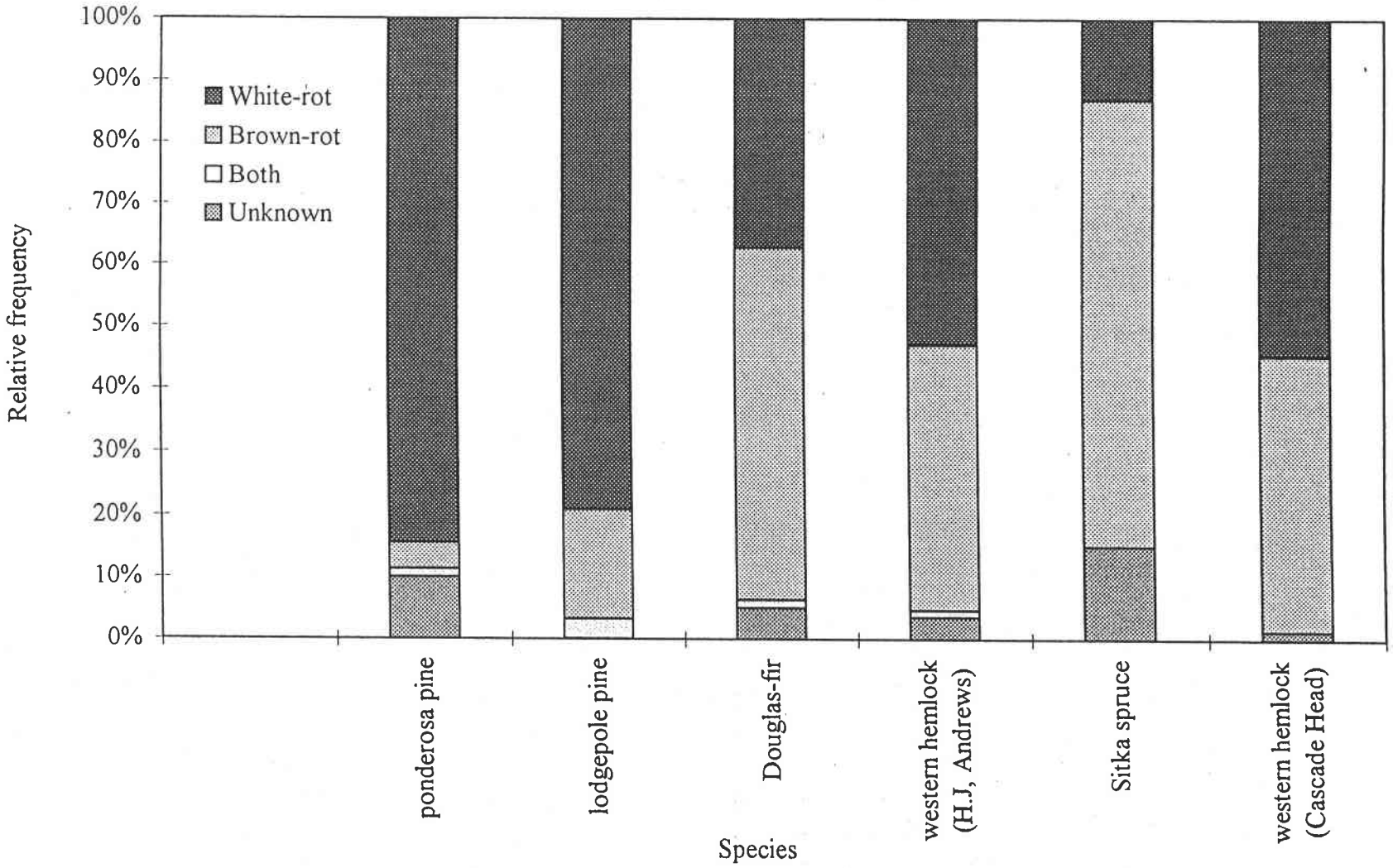

Figure 2-5. Relative frequency of type of rot in the wood component of roots.

decomposing western hemlock roots at both CAH and HJA. It appeared that neither white-rots nor brown-rots decomposed resin cores.

2.4.3 Decomposition of whole roots

2.4.3.1 Density changes over time

Species separated into two major root decomposition patterns over time. For lodgepole pine, Douglas-fir, and Sitka spruce, the density of whole roots decreased in the early decomposition stage and then tended to remain constant as decomposition progressed (Figure 2-6). In contrast, root density of western hemlock and ponderosa pine continually decreased until all components of roots were decomposed (Figure 2-6).

2.4.3.2 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 to the 7% and 11% frequencies of resin cores in western hemlock and ponderosa pine (Table 2-5). 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 the two distinct decomposition patterns of woody roots. Species having slow rates of density change in later decomposition stages had a high proportion of bark. These species included Sitka spruce and Douglas-fir. An exception was lodgepole pine which had a relatively low bark fraction. Western hemlock and ponderosa pine, which showed a steady decrease in root density, contained a small fraction of bark in their roots.

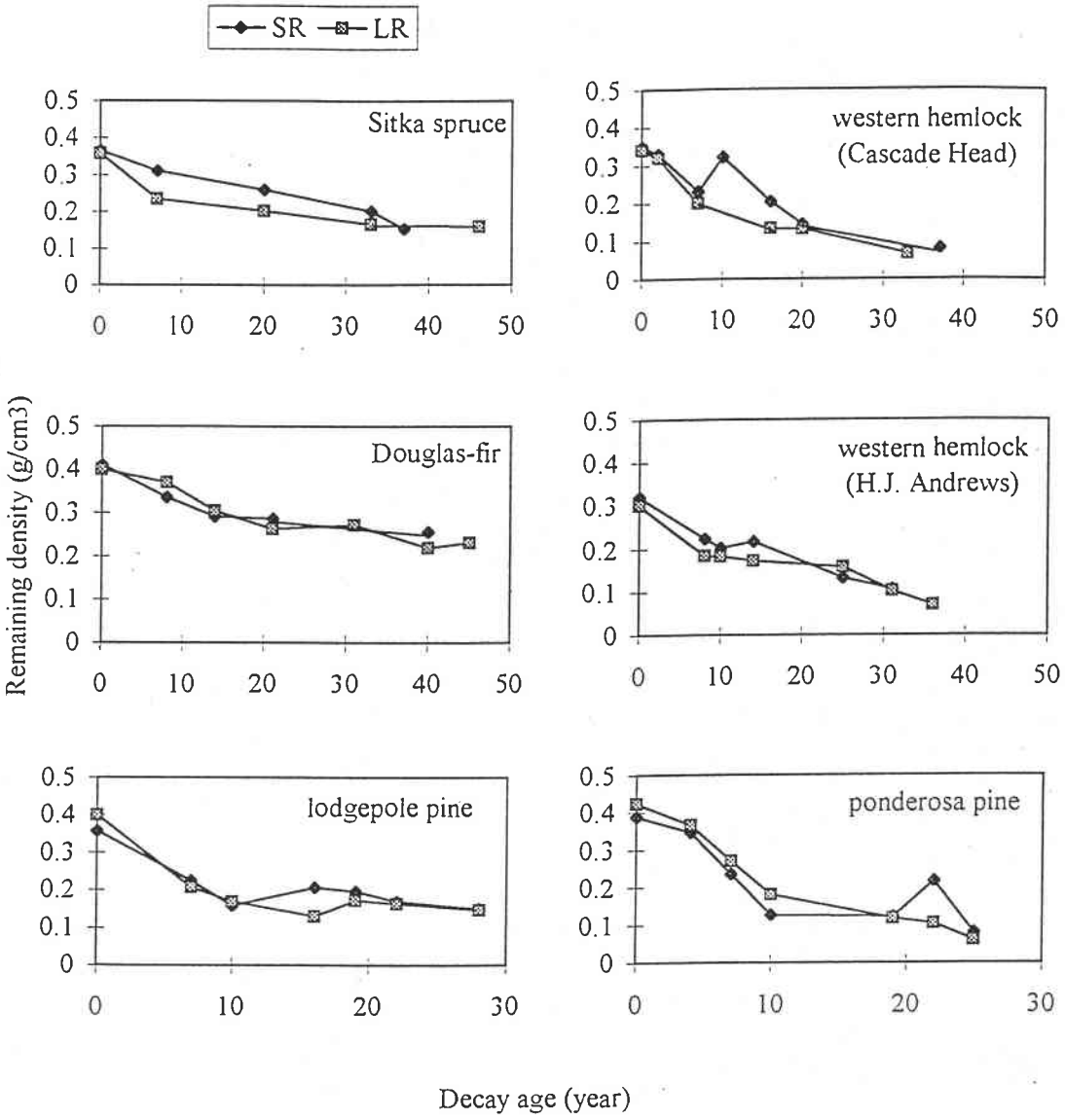

Figure 2-6. Density change over time of whole woody roots*.

* SR, small roots; LR, large roots.

Table 2-5. Frequency and volume proportions of resin cores and bark in woody roots*.

Site	Species	Resin cores		Bark
		Frequency (%)	Volume proportion of roots (%)	Volume proportion of 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)	22.5 (10.1)
Pringle Falls	ponderosa pine	11	10.8 (5.6)	30.7 (14.8)

* the value in parenthesis is standard error.

2.4.3.3 Decomposition rate-constant of whole roots

The species with resin cores had lower decomposition rate-constants than those of without resin cores (Table 2-6). This result confirmed the hypothesis that the decomposition rate-constant of woody roots could be explained by its structural component composition, especially the presence of resin cores. The single-exponential model was a good predictor of the density of woody roots without resin cores. In contrast, this model was relatively poor in predicting the decomposition of woody roots with resin cores (Table 2-6). There were significant differences in decomposition rate-constants of woody roots among the species even when root size was similar ($F = 10.13$, $P < 0.05$) (Figure 2-7). The order of increasing woody root decomposition rate-constants was: Douglas-fir < Sitka spruce < lodgepole pine < western hemlock (HJA) < western hemlock (CAH) < ponderosa pine.

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 (Table 2-6 and Table 2-7). The R^2 of the regressions for Sitka spruce, Douglas-fir, and lodgepole pine was above 0.93, except for 0.8 for small roots of Douglas-fir. The decomposition rate-constants of labile fraction of woody roots for these three species were 0.035-0.127, 0.035-0.087, and 0.086-0.090/year, respectively. The decomposition rate-constant of slow fraction of woody roots ranged from 0.0001 to 0.004, at least an order of magnitude lower than the rates of the fast fraction of woody roots.

No significant differences in decomposition rate-constants were observed between the two size classes (small *vs.* large roots) of the species examined (Figure 2-7). This result differed from one of our initial hypotheses in that we expected the decomposition rate-constant to decrease with increasing root diameter. Our results indicated that changes in surface area:volume ratio with size as well as the rates of fungal colonization had less influence than anticipated.

Table 2-6. Coefficients of regressions of single-exponential model used to estimate decomposition rate-constant (k) of roots of dominant coniferous species in the Pacific Northwest.

Site	Species	Type	Diameter (cm)	Regression coefficients[a]			
				Y_0 (g/cm^3)	k (/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

[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. * $0.05 > P > 0.01$; ** $P < 0.01$.

[b] Each data point represents the mean of 3 - 12 samples.

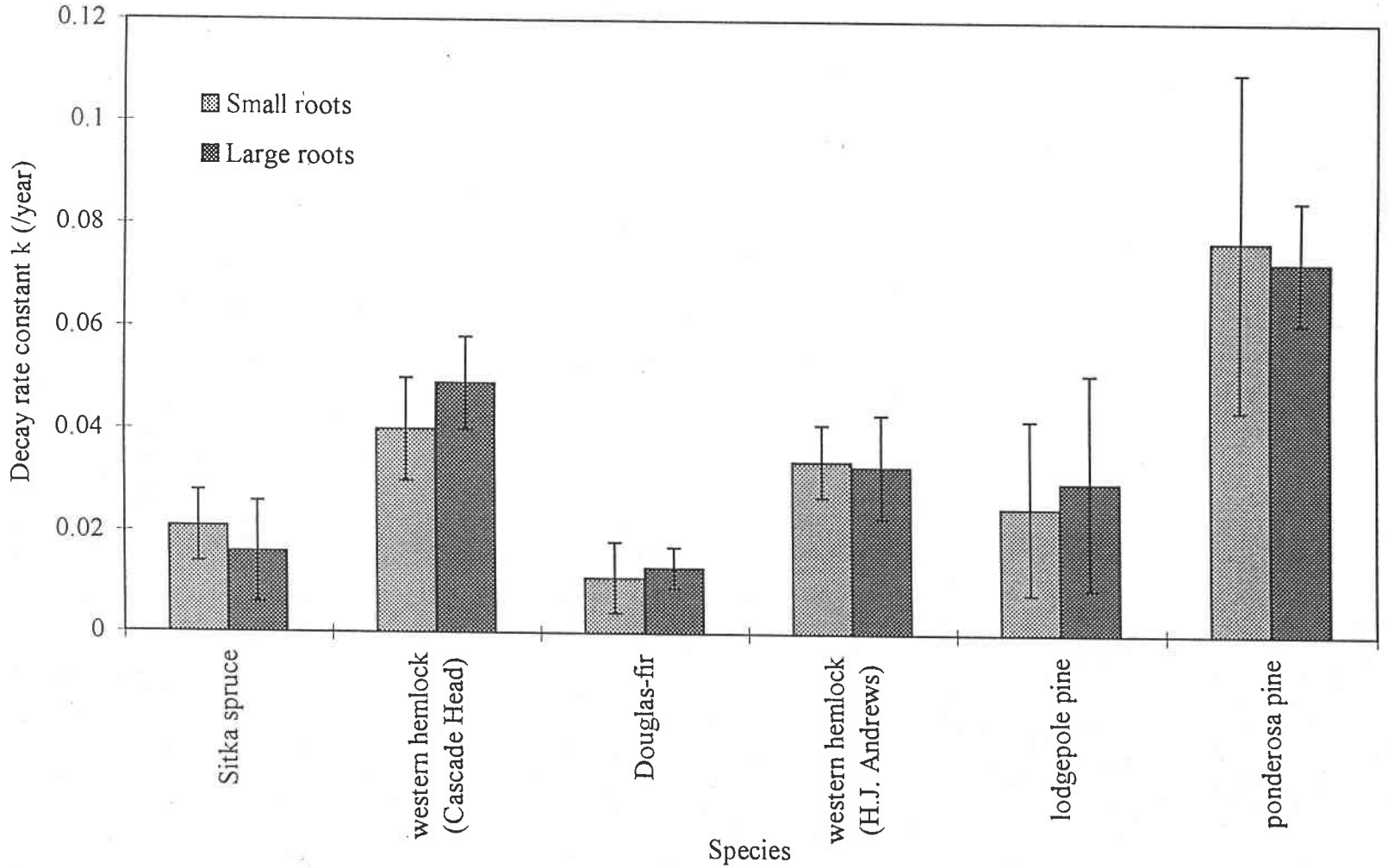

Figure 2-7. Confidence interval of decomposition rate-constant of whole roots.

Table 2-7. Coefficients of regressions of double-exponential model used to estimate decomposition rate-constant of woody roots with resin cores in the Pacific Northwest.

Site	Species	Type	Diameter (cm)	Regression coefficients					
				Y_{slow} (g/cm^3)	ks (/year)	Y_{fast} (g/cm^3)	kf (/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 $Y_t = Y_{slow}\, e^{-(ks^* t)} + Y_{fast}\, e^{-(kf^* t)}$ where Y_t is the density of roots at time t (years), Y_{slow} and Y_{fast} are the initial relative density of slow decomposition-fraction and fast decomposition-fraction of roots, and ks and kf are the decomposition rate-constants of these two fractions.

[b] Each data point represents the mean of 3 - 12 samples.

2.4.3.4 Control of initial substrate quality

No clear interspecific or size differences were observed in the initial carbon concentration of roots (Table 2-8). Initial carbon concentrations among the roots ranged from 50.7 to 54.4%. Large roots of western hemlock (HJA) and ponderosa pine possessed the highest C:N ratio, up to 313 and 284. Small roots of ponderosa pine had highest nitrogen concentration (0.34%) and thus the lowest C:N ratio (149).

Except for western hemlock (HJA), water-soluble phenolics were higher in small than large roots. Concentration of nonpolar extractable (NPE: fats, oils and waxes) did not have a clear pattern among different size roots. Nor did acid-soluble carbohydrate change very much with different species and size. Lignin concentrations were relatively low in roots of ponderosa pine and high in Douglas-fir, although size of roots did not show clear correlation with lignin concentration. Lignin: N ratio of these woody roots ranged from 80 to 154 (Table 2-8).

Whole root decomposition rate-constants were not significantly correlated to any of the 13 initial chemical quality indices of dead roots examined in our study (Table 2-9). Of the indices examined, NPE (nonpolar extractives) and lignin concentrations showed the best correlation with decomposition rate-constants of woody roots, although the relationship was not significant ($P = 0.15$). The determination coefficients (R^2) of C:N, lignin: N and water-soluble phenolics and decomposition rate-constants only reached 0.18, 0.08, and 0.13, respectively.

2.4.3.5 Climatic effects

The degree that climate influenced decomposition rate-constants of tissues for the different species could only be assessed for western hemlock which occurred at both CAH and HJA sites. The decomposition rate-constants of western hemlock woody roots were higher at CAH than HJA regardless of root size (Table 2-6). However, no significant differences of decomposition rate-constants of western hemlock woody roots between two sites were found (Figure 2-7).

Table 2-8. Chemical characteristics of fresh woody roots for two size classes*.

Species	Size	% N	% C	C:N	% NPE	% WS sugar	%WS phenols	%AS Cellulose
lodgepole pine	Large	0.28	51.6	183.4	7.7	1.3	0.88	50.0
ponderosa pine	Large	0.18	51.1	283.9	16.6	1.2	0.76	50.4
Douglas-fir	Large	0.27	50.9	187.0	1.9	1.4	2.12	58.3
western hemlock	Large	0.16	50.0	312.6	8.8	7.6	8.16	42.1
lodgepole pine	Small	0.21	51.8	241.4	13.5	2.6	1.24	47.6
ponderosa pine	Small	0.34	51.1	149.0	6.0	2.1	1.93	58.8
Douglas-fir	Small	0.27	51.6	190.1	5.7	2.2	4.26	49.8
western hemlock	Small	0.25	50.8	201.9	2.7	1.4	4.23	56.6

Species	Size	%AIS lignin	%(Lignin+ cellulose)	Lignin:N ratio	Cellulose : N ratio	LCI ratio	(Lignin+ cellulose) N ratio
lodgepole pine	Large	36.5	86.5	129.9	177.6	0.42	307.4
ponderosa pine	Large	27.7	78.1	154.0	279.9	0.35	433.9
Douglas-fir	Large	32.3	90.5	118.5	214.2	0.36	332.8
western hemlock	Large	24.5	66.6	153.2	263.1	0.37	416.3
lodgepole pine	Small	30.1	77.7	140.5	222.1	0.39	362.6
ponderosa pine	Small	27.5	86.3	80.3	171.4	0.32	251.6
Douglas-fir	Small	34.3	84.1	126.4	183.8	0.41	310.2
western hemlock	Small	31.3	87.9	124.6	224.9	0.36	349.6

* N, nitrogen;
C,carbon;
NPE, nonpolar extratables (fats, oils, and waxes);
WS sugar, water soluble carbonhydrate;
WS phenols, water soluble phenols, expressed as % tannic acid equivalents.
AS cellulose, acid soluble cellulose and hemicellulose;
AIS lignin, acid insoluble part including lignin and other recalcitrant carbon, refer to lignin here;
Lignin and cellulose in LCI ratio=Lignin:(cellulose+lignin) refer to AIS lignin and AS cellulose;
Lignin and cellulose in (Lignin + cellulose) index and (Lignin + cellulose) : N ratio refer to AIS lignin and AS cellulose.

Table 2-9. Effects of different initial substrate index on decomposition rate-constant of woody roots*.

Initial substrate index	F	df	*P*	R^2
Carbon	2.57	1, 7	0.16	0.30
Nitrogen	0.60	1, 7	0.47	0.09
Carbon: Nitrogen ratio	1.33	1, 7	0.29	0.18
NPE	2.75	1, 7	0.15	0.31
WS sugar	0.00	1, 7	0.96	0.00
WS polyphenol	0.91	1, 7	0.38	0.13
AS cellulose	0.01	1, 7	0.92	0.01
AIS lignin	2.66	1, 7	0.15	0.31
Lignin + cellulose	0.64	1, 7	0.45	0.10
Lignin : N ratio	0.53	1, 7	0.49	0.08
Cellulose : N ratio	1.84	1, 7	0.22	0.23
(Lignin + cellulose): N	1.30	1, 7	0.30	0.18
LCI ratio	1.79	1, 7	0.23	0.23

* NPE, nonpolar extratables (fats, oils, and waxes);
WS sugar, water soluble carbonhydrate;
WS phenols, water soluble phenols, expressed as % tannic acid equivalents.
AS cellulose, acid soluble cellulose and hemicellulose;
AIS lignin, acid insoluble part including lignin and other recalcitrant carbon, refer to lignin in this study.
Lignin and cellulose in LCI ratio=Lignin:(cellulose+lignin) refer to AIS lignin and AS cellulose;
Lignin and cellulose in (Lignin + cellulose) index and (Lignin + cellulose) : N ratio refer to AIS lignin and AS cellulose.

2.4.3.6 Effects of soil nitrogen availability

The ion exchange resin bags indicated there were significant differences in soil nitrogen availability among the three sites, as estimated by soil ammonium availability (P = 0.007) (Table 2-10). Soil ammonium availability of CAH was 98.99 ug/g air-dry resin, the highest among three sites. HJA and PRF had very similar soil ammonium availability values and showed significantly lower nitrogen availability than CAH. In contrast, there was no clear difference of soil nitrate availability index among three sites (P = 0.30), which ranged from 2.75 to 9.97 ug/g air-dry resin. The soil nitrogen availability index which combines NH_4^+ + NO_3^- showed significant differences among three sites (P = 0.01), that was consistent with the pattern of soil NH_4^+ availability among three sites. The decomposition rate-constant of woody roots was not correlated with soil ammonium availability (P = 0.19, R^2 = 0.31), despite the differences observed between sites. Moreover, the fastest decomposing woody roots, ponderosa pine, occurred at the lowest nitrogen availability site.

2.4.4 Carbon and nitrogen dynamics

2.4.4.1 Carbon loss

The pattern of carbon loss during woody root decomposition was very similar to that of mass loss (Figure 2-8). The similarity of these two curves was due to the consistent carbon concentration of roots during decomposition, which was around 50% of dry weight as reported by other studies of wood detritus (Chen and Xu, 1992; Harmon and Chen, 1991; Harmon et al., 1986). In order of increasing carbon loss percentage of woody roots after 20 years of decomposition was: Douglas-fir(21%)< Sitka spruce (32%) < lodgepole pine (43%) < western hemlock (HJA 49%) < western hemlock (CAH 59%) < ponderosa pine (78%), the same order as the decomposition rate-constants.

Table 2-10. Soil nitrogen availability index among three sites*.

Site	Nitrogen Availability Index (ug/g air-dry resin)		
	$NH4^+$	$NO3^-$	$NH4^+ + NO3^-$
Cascade Head	98.99[a] (59.08)	8.06[a] (9.74)	107.05[a] (59.14)
H.J. Andrews	19.07[b] (8.12)	2.75[a] (0.65)	21.82[b] (7.8)
Pringle Falls	19.10[b] (17.53)	9.97[a] (6.25)	29.07[b] (21.53)

*: the number in parenthesis is standard error. Values in a column followed by a different letter are significantly different ($P < 0.05$).

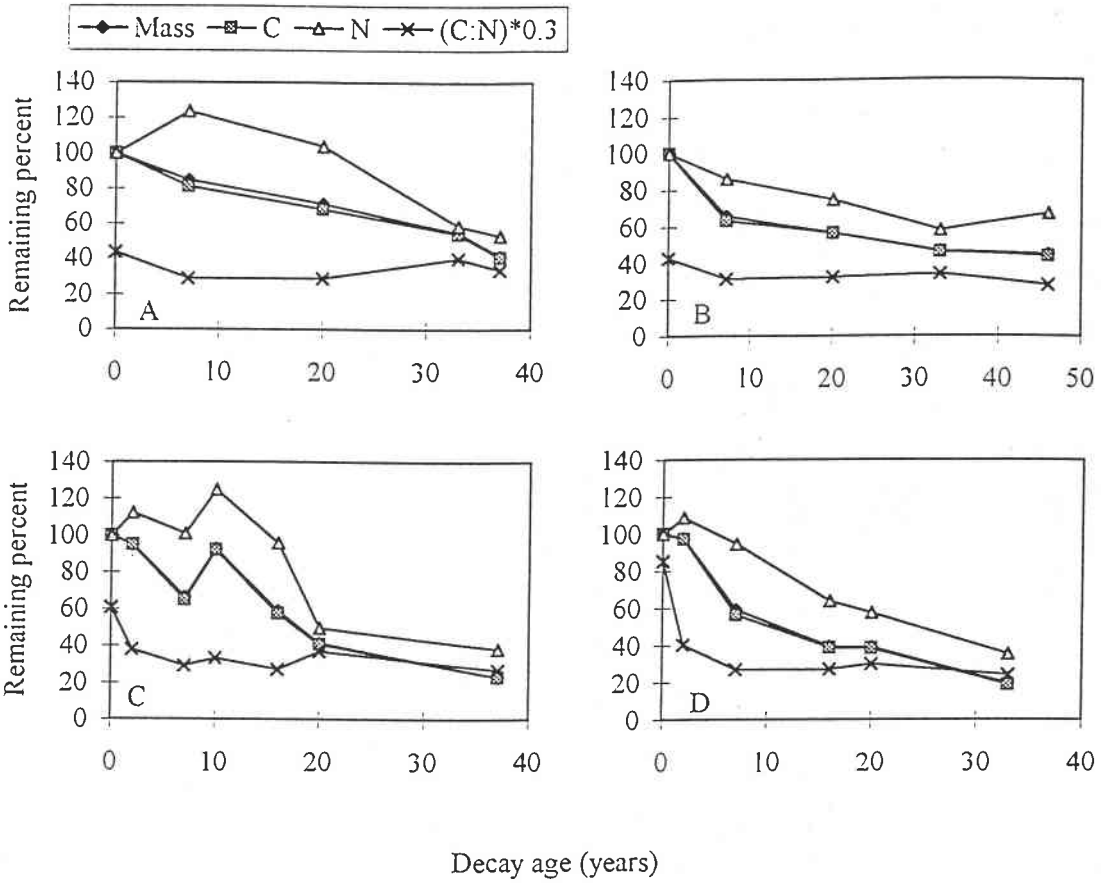

Figure 2-8a. Mass, C, and N dynamics in root decomposition at Cascade Head site*

*: (A) Sitka spruce small roots; (B) Sitka spruce large roots; (C) western hemlock small roots; and (D) western hemlock large roots.

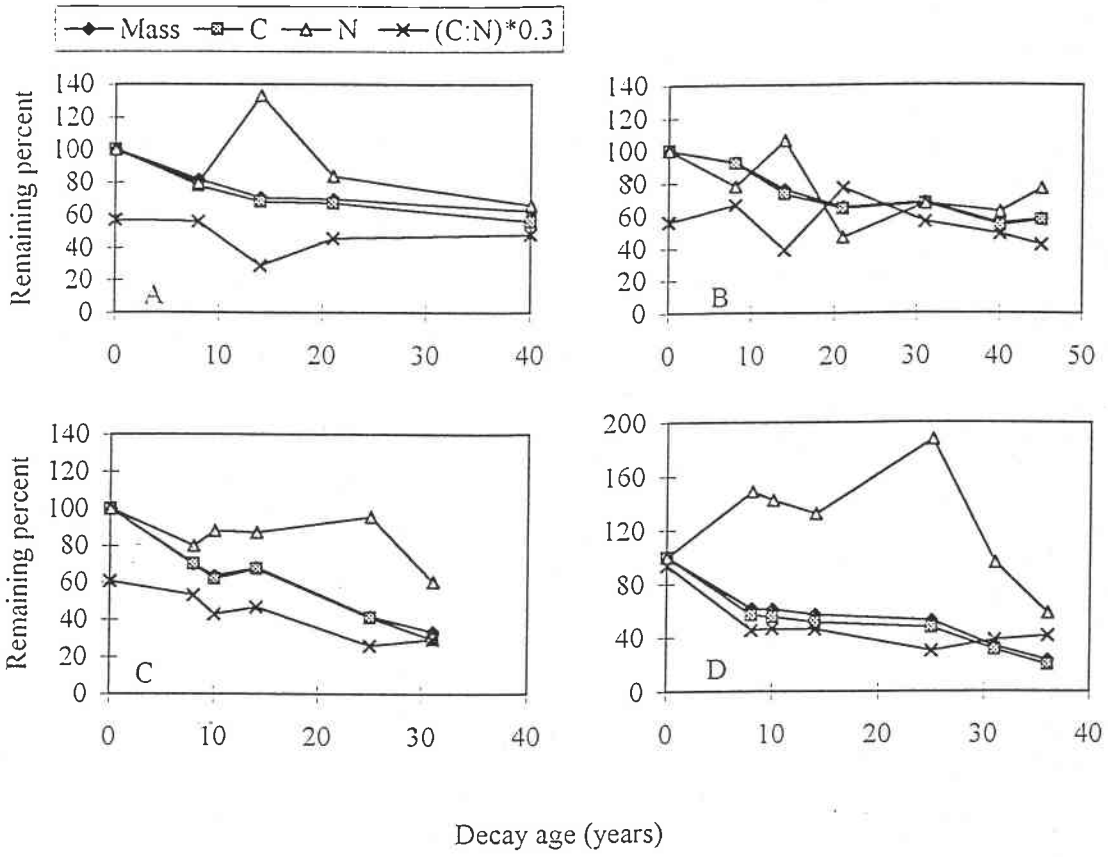

Figure 2-8b. Mass, C, and N dynamics in root decomposition at H.J. Andrews site*.

*: (A) Douglas-fir small roots; (B) Douglas-fir large roots; (C) western hemlock small roots; and (D) western hemlock large roots.

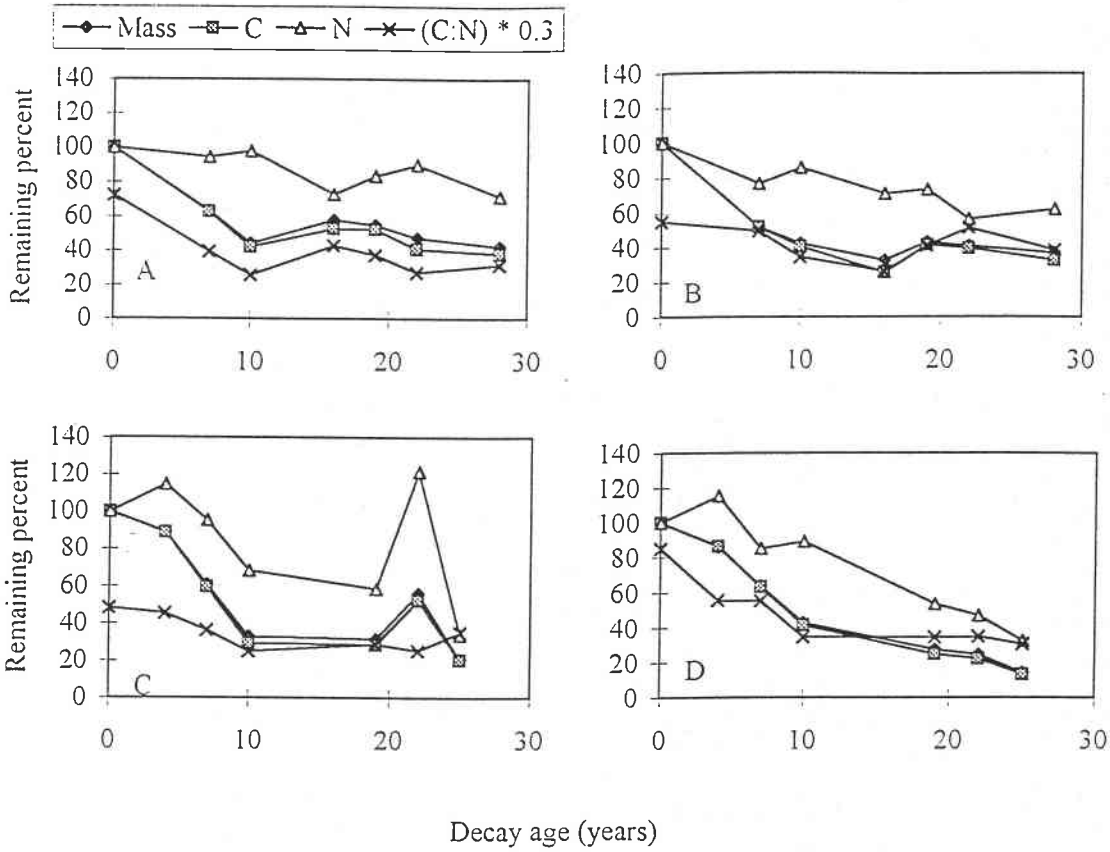

Figure 2-8c. Mass, C, and N dynamics in root decomposition at Pringle Falls site*.

*: (A) lodgepole pine small roots; (B) lodgepole large roots; (C) ponderosa pine small roots; and (D) ponderosa pine large roots.

2.4.4.2 Nitrogen dynamics

Two patterns of nitrogen dynamics existed during woody root decomposition (Figure 2-8). The most common pattern was for nitrogen content of woody roots to show a consistent declining trend over time after a short phase of nitrogen accumulation in the earliest decay stage (Figure 2-8a, Figure 2-8c). Sitka spruce, western hemlock, lodgepole pine, and ponderosa pine at CAH and PRF had this pattern. A less common nitrogen dynamic appeared in both size roots of Douglas-fir and small roots of western hemlock at HJA (Figure 2-8b). The nitrogen content of these woody roots decreased in the early stages of decomposition, then increased during the middle decomposition period, and then the nitrogen content declined with extensive decomposition. For example, the nitrogen content of Douglas-fir was 106-133% of the initial nitrogen content after 14 years of decomposition. Nitrogen accumulation, to a great extent, occurred in large roots of western hemlock at HJA (Figure 2-8).

Nitrogen was lost from woody roots more slowly than mass or carbon (Figure 2-8). Species differed markedly in the total net nitrogen released during decomposition with fast decomposing species releasing more nitrogen than slow decomposing species. For example, ponderosa pine roots released almost half of their initial nitrogen during the first 25 years of decomposition. In contrast, Douglas-fir roots lost less than 20% of total initial nitrogen content during the same time period.

The trend in nitrogen dynamics of decomposing roots was more clearly displayed by plotting the change in nitrogen content versus mass loss (Figure 2-9). Root mass loss was positively correlated with nitrogen 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 $N_{loss} = a + b^* M_{loss} + C^*M_{loss}^2$ where N_{loss} is nitrogen loss percentage and M_{loss} is the mass loss 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 nitrogen dynamics of the four species at CAH and PRF clearly showed that

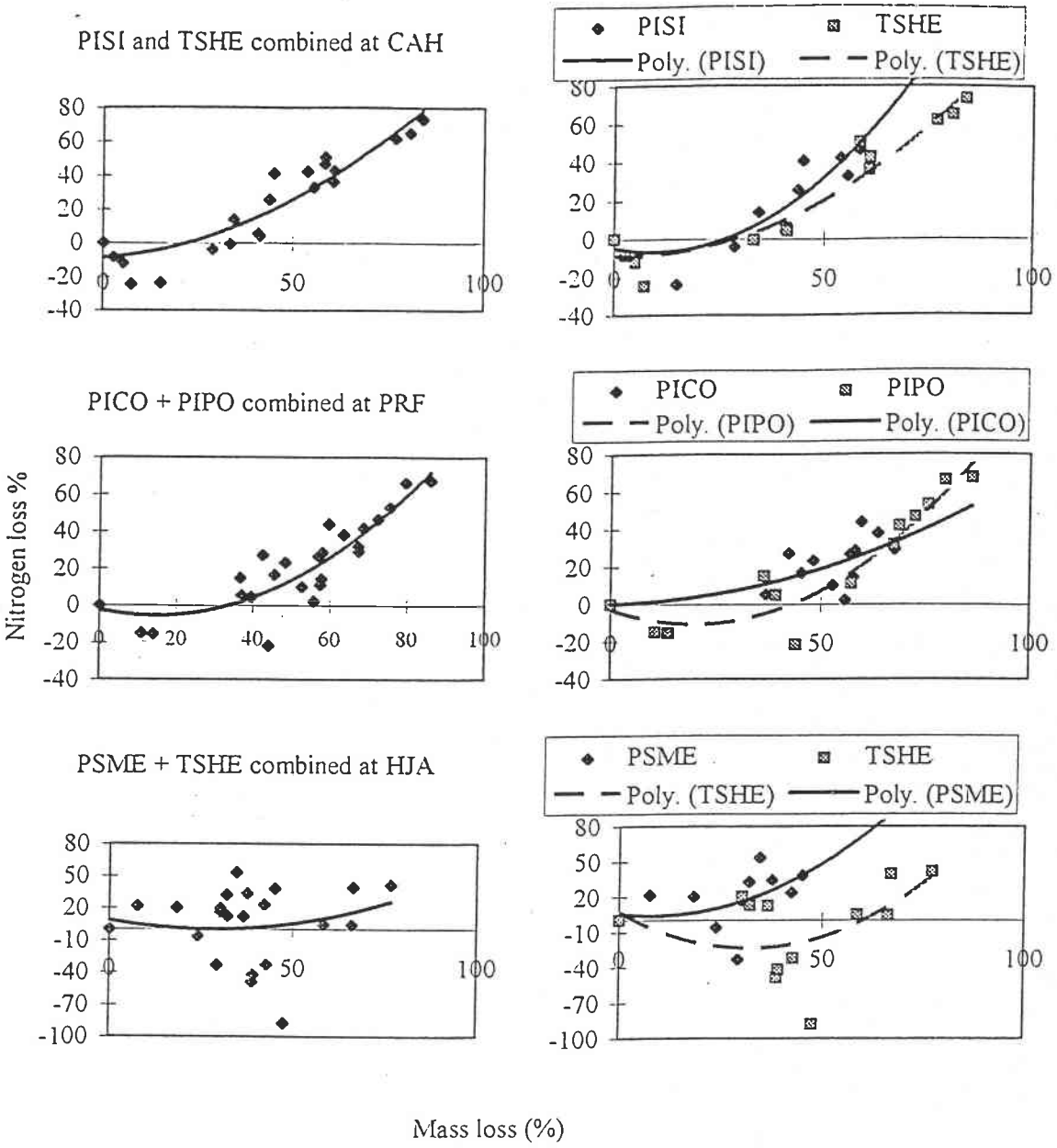

Figure 2-9. Nitrogen content dynamics during root mass loss at three sites*.

* PISI-- Sitka spruce; TSHE-- western hemlock; PSME--Douglas-fir; PICO-- lodgepole pine; and PIPO--ponderosa pine.

the dead woody roots released nitrogen after 20-30% of the 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 (Figure 2-8). At CAH, C:N ratio of large woody roots of Sitka spruce dropped from 142 to 94 after 46 years of decomposition. C:N ratio of western hemlock large roots decreased from 312 to 139 at HJA. Similarly, the C:N ratio of ponderosa pine large roots decreased from 284 to 104. Surprisingly, most C:N ratio of very decomposed roots was still higher than 80 after several decades of decomposition and, despite these high values, nitrogen was released.

2.5 DISCUSSION

2.5.1 Controls of woody root decomposition

2.5.1.1 Structural components, initial substrate quality, 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 fastest decomposition rate-constant; root bark the second; and the resin cores the slowest. The decomposition of woody roots is the integrative result of mass loss of each individual structural component of roots. Different species varied in the structural components of woody roots which directly influenced their decomposition pattern. 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 further decomposition. The decomposition rate-constants of these species were low, ranging

from 0.011 to 0.030/year. In contrast, 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 decomposition rate-constants, ranging from 0.033 to 0.077/year. Our study suggests the proportion of root structural components plays critical roles in determining the decomposition rate of species, a factor that should be accounted for in models of woody root decomposition.

In contrast, initial substrate quality indices were not useful predictors of woody root decomposition rate-constants. None of the 13 initial substrate indices including the C:N, lignin:N ratios, and polyphenol concentrations, was correlated significantly to the decomposition rate-constant of whole roots in the Pacific Northwest (Table 2-9). Although initial substrate indices such as lignin:N and C:N ratios are widely regarded as the best predictors of decomposition rates (Berg, 1984; Fogel and Cromack, 1977; Hobbie, 1996; Melillo et al., 1982), most of these studies were targeted at fine litter and for short term periods. Decomposition of dead wood is only grossly similar to fine litter making it difficult to extrapolate from the latter form of detritus (Harmon and Chen, 1991). For example, white-rots, which degrade lignin, were dominant in the decomposition of woody roots of ponderosa pine and lodgepole pine (Figure 2-5). Thus the entire conceptual basis for using the lignin : nitrogen ratio or lignin-cellulose index as indicators of substrate quality is called into question (Aber et al., 1990; Melillo et al., 1982). Moreover, the decomposition of woody roots takes decades in temperate forests (Fahey et al., 1988; Waid, 1974; Yavitt and Fahey, 1982; and this study). The impact of initial substrate quality on the decomposition of woody roots probably is mainly limited to the early decomposition stages with diminished effects in the later decomposition stages. Furthermore, the control of substrate litter quality on decomposition changes over time. Berg and Staaf (1980) showed a shift from nutrient control in the early stages of decomposition of *Pinus sylvestris* needles, to the dominance of lignin as the controlling factor in later stages. This probably is true in woody root decomposition as well.

Did the rot types occurring in woody roots have anything to do with their root structural components? Different species of woody roots were degraded by different rot types. In our study, the white-rots occurred both in lodgepole pine root wood which had resin cores and ponderosa pine root wood which did not. Brown-rots happened to appear in root wood of Douglas-fir and Sitka spruce, both possessing resin cores in their woody roots. Thus no apparent relationships between rot types of woody roots and root structural component composition were indicated in our study. However, we did find white-rots frequently occurred at PRF which had lowest soil nitrogen availability among three sites whereas brown-rots appeared in CAH and HJA which had higher soil nitrogen availability (Table 2-10). This confirms previously studies where white-rots were more common in soils with low level of available nitrogen and brown-rots appeared frequently in relatively high soil nutrient availability stands (Hammel, 1997; Paul and Clark, 1989; Panshin and Zeeuw, 1980), although the factors that determine rot types of woody roots are not fully understood yet.

Root size did not influence the decomposition rate-constants of woody roots or component parts significantly in our study (Figure 2-7). 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 diameter variability of woody roots at 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. 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 root decomposition of red spruce, beech, yellow birch in a northern hardwood ecosystem.

The single-exponential model has been used widely to model root decomposition (Bloomfield et al., 1993; Yavitt and Fahey, 1982). 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 (Figure 2-10). The double-exponential model solves this problem by modeling both fast and slow decomposition phases. The double-exponential model indicated a much better fit of the remaining density of lodgepole pine roots than the single-exponential model, especially well in later decomposition stage (Figure 2-10). 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.

2.5.1.2 Climatic effects

Abiotic factors with the potential to influence root decomposition include temperature, moisture, oxygen concentration, and soil properties such as texture. Of these, temperature and moisture content are regarded as the main abiotic factors influencing root decomposition (Heal et al. 1997; Santantionio and Grace 1987; Swift et al. 1979). The result that decomposition rate-constant of western hemlock was slightly higher at CAH than HJA (Table 2-6 and Figure 2-7) suggested that the environment may be slightly more favorable for root decomposition at CAH than HJA. These differences in decomposition rate-constant may be attributed to the fact the CAH site has milder and more humid environment than the HJA site. However, the fact that the fastest decomposing species, ponderosa pine, occurred at the most unfavorable environment site (PRF) and the slowest decomposing species Douglas-fir occurred at a mild site (HJA) suggests the influence of root substrate quality overrides climate effects in the Pacific Northwest. An independent evaluation of the climatic effects on decomposition of woody roots was difficult using the chronosequence method because species were confounded with the climate of each site.

2.5.2 Nitrogen dynamics

We hypothesized that decomposing woody roots would experience a long nitrogen 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 nitrogen

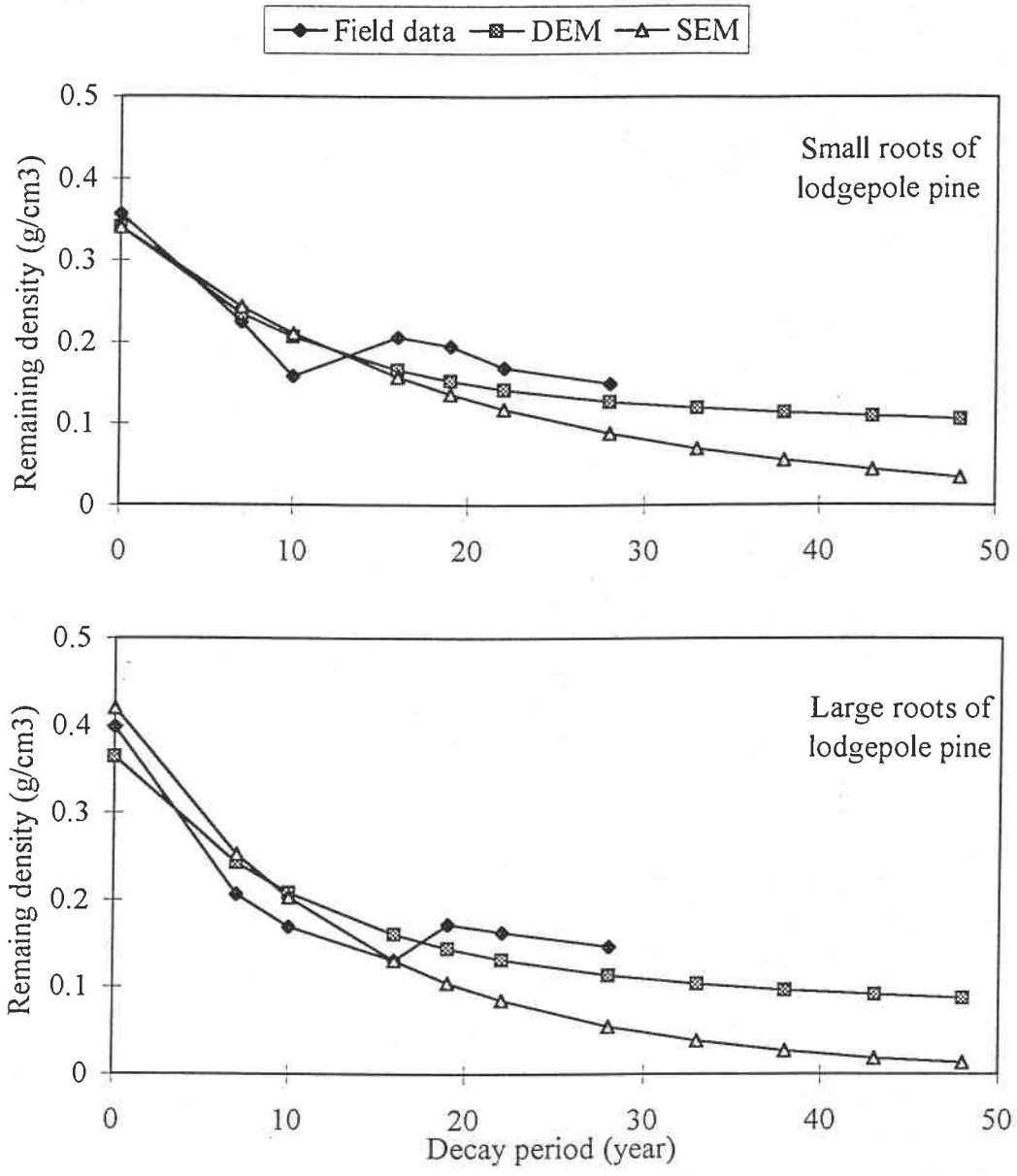

Figure 2-10. Comparsion of single-exponential and double-exponential models*.

*: DEM, double-exponential model; SEM, single-exponential model.

release as observed in most fine litter decomposition studies (Aber et al., 1990; Berg and Ekbohm, 1983; Gosz et al., 1973; Melillo et al., 1982; Staaf and Berg, 1981). Contrary to this hypothesis, patterns of nitrogen release from decomposing woody roots at early decomposition stages at CAH and PRF were observed, consistent with those obsereved in several other root decomposition studies. In our study, dead root started to release nitrogen at a high average C:N ratio of 140. Parker et al. (1984) found nitrogen 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 nitrogen at the start of root decomposition with an initial C:N ratio 90. Hobbie (1996) found several Alaska tundra roots of shrub and trees with initial C:N ratio of 30 to 50 lost nitrogen immediately following incubation in microcosms, although some nitrogen immobilization occurred in the later decomposition stages. These studies indicated that dead roots, unlike other litters, did not have a long nitrogen accumulation period in decomposition (Aber et al., 1990; Berg and Ekbohm, 1983; Gosz et al., 1973; Melillo et al., 1982; Staaf and Berg, 1981). In contrast, they tend to release nitrogen much earlier at a high C:N ratio.

The concept of the "critical C:N ratio" refers to the C:N ratio at the point of maximum nitrogen accumulation (McClaugherty et al., 1985). After this point is reached the litter starts to release nitrogen. According to this concept, the critical C:N ratio of woody roots at the Pacific Northwest was between 100 to 180. 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 wood. One reason for high critical ratio of dead roots has to do with the nature of their carbon constituents. Dead woody roots generally contain more recalcitrant carbon and less labile carbon than fine roots (Chen and Harmon, unpublished data; McClaugherty et al., 1984) and other fine litter (Fogel and Cromack, 1977; Melillo et al., 1982). Microbes prefer energy rich and easily decomposable labile carbon over recalcitrant organic matter. Therefore labile carbon in woody roots may be less available than the carbon in fine litters. This would allow nitrogen to be released at a far higher C:N ratio

in the former substrate. From this viewpoint, the use of total carbon in critical C:N ratio calculation may not be appropriate. Instead, use of labile carbon or microbially available carbon of organic matter may be more appropriate than total carbon.

Nitrogen released from decomposing woody roots may be controlled by factors more than critical C:N ratios. Harmon et al. (1994) reported several nitrogen loss pathways including fragmentation, absorption from mycorrhizae and roots, leaching, insects, and fungal sporocarps that remove nitrogen 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 nitrogen budget from organic sources such as dead roots (Turnbull et al., 1996). Since bark nitrogen concentrations were much higher than wood (Chen and Harmon, unpublished data), fragmentation of bark could also contribute to nitrogen loss. Leaching is another possible pathway of nitrogen released from decomposing roots, especially at CAH site because of high precipitation.

2.5.3 Management implications

Decomposition of woody roots in coniferous forest ecosystems in the Pacific Northwest is not only an important link in carbon and nitrogen cycling but also has management implications for evaluating soil strength, providing belowground habitat, and playing roles in forest growth and nutrient conservation.

The presence of woody roots in soils directly influences soil strength. The decomposition of woody roots, to some degree, decreases soil strength, which may enhance the odds of soil erosion and landslide, especially on steep slopes (Burroughs and Thomas, 1977; Gray and Megahan, 1981; Swanson et al., 1987; Wu et al., 1979). The mechanical reinforcement provided by the living woody root system diminishes over time when roots start to decompose. The occurrence of decay-resistant resin cores in woody roots slows down the decomposition of roots, which in turn prolongs the functional period of woody roots to maintain soil strength. Root decomposition reduces both the number and strength of roots holding the soil together. Our root decomposition study provides the basis to evaluate the roles of dead roots in soil

strength. For example, ponderosa pine, the fastest decomposing roots in our study, lost its root reinforcement power more quickly than Douglas-fir roots which showed the slowest rates. Furthermore, the dead woody roots in young forests may be more susceptible to losing their strength faster than old-growth forests because young forests produce more small roots with fewer resin cores than old-growth forests. Although it is known that soil erosion and landslides are the interactive result of many complicated factors such as geologic and climatic elements (Swanson et al. 1986), root decomposition data may be useful to prevent or predict soil erosion and landslides in the Pacific Northwest.

Decomposing woody roots of forests also create many belowground channels, which in turn may provide habitats for soil animals and wildlife. Due to the slow decomposition of root bark, it is common to find many hollow dead roots in forest soils. These decomposing woody roots vary not only in number and decay states but also in sizes, creating a diversity of root habitats in forest soil. Several species rely on or at least use decomposing roots as their habitats or movement channels in Douglas-fir forests of western Cascade of Pacific Northwest. These species include 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 (Hayes, personal communications 1998).

In general, the nitrogen release from dead woody roots appears to synchronize with the demand of new forest growth. Forest harvests, especially clear-cuts, create as much as 200 Mg/ha of dead roots in the Pacific Northwest (Vogt et al., 1986). Although the nitrogen concentration of woody roots is low, the total amount of nitrogen associated with roots may be large because of the large mass of dead roots. According to our study, the release of nitrogen after 4 - 7 years of woody root decomposition matches the demand of forest growth if forest regeneration is good. This synchrony may be important for sustainable development of forest ecosystems in the Pacific Northwest. If seedlings are not established in a timely manner, they will not be able to act as sinks for this nitrogen release during root decomposition. Then it may

cause a net loss of nitrogen from the system. Therefore a rapid regeneration after forest harvests is important.

2.6 CONCLUSIONS

The order of increasing woody root decomposition rate-constants (k) among the species were Douglas-fir < Sitka spruce < lodgepole pine < western hemlock < ponderosa pine. Western hemlock and ponderosa pine generally did not have resin cores in their woody roots, showing a high k of 0.033 to 0.077/year, respectively. In contrast, those species with resin cores Sitka spruce, Douglas-fir, and lodgepole pine had a much lower k, ranging from 0.011 to 0.03/year. Our study indicated that a structural component approach provided a better estimation of long-term mass loss than did initial substrate quality indices. None of the 13 initial substrate quality indices examined was significantly correlated to decomposition rate-constants. Differences in woody root substrate quality corresponded more closely to its physical structures than chemical indices. Root size did not appear to influence root decomposition among the five species examined. The double-exponential model was a better fit than the single-exponential model for woody roots with resin cores, while the single-exponential model was sufficient for species without resin cores. The effects of climate on root decomposition were apparently overridden by differences in species. Rot types in dead roots varied with species, with the lodgepole pine and ponderosa pine dominated by white-rots, Douglas-fir and Sitka spruce dominated by brown-rots. Both rot types appeared in roots of western hemlock.

In general, decomposing roots started to release nitrogen after 20-30% mass loss at a point when the average C:N ratio was as high as 140. Therefore, coniferous woody roots had a much higher critical C:N ratio than observed in other litters. The fastest decomposing species, ponderosa pine, released almost half of its initial nitrogen store in the first 25 years. In contrast, the slowest decomposing species, Douglas-fir, released less than 20% of initial nitrogen over the same time period. Root decomposition has management implications for evaluating soil strength, providing belowground habitat, and playing roles in forest growth and nutrient conservation.

2.7 ACKNOWLEDGMENTS

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CHAPTER 3

MASS, C, AND N DYNAMICS OF DECOMPOSING ROOTS IN CONIFEROUS FORESTS OF THE PACIFIC NORTHWEST: A TIME SERIES APPROACH

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3.1 ABSTRACT

Woody root decomposition was studied in Sitka spruce, Douglas-fir, and ponderosa pine forests at Cascade Head, H. J. Andrews, and Pringle Falls Experimental Forests in Oregon, using a time series approach. For fine and small roots, species significantly influenced mass loss during the first 2 years of decomposition. In contrast, there were no significant species effects on the decomposition of medium, large, jumbo roots. For the same period, site differences had little impact on decomposition of roots, regardless of root size. For fine roots, Oregon ash was the fastest among the 15 species examined during two years of decomposition, losing about 63% of its initial mass. Incense-cedar had the slowest decomposition, losing about 35% of initial mass in the same period. All fine roots had a period of rapid mass loss during the first 3 to 6 months, which accounted for more than 50% of the mass loss in the first two years. For small roots, ponderosa pine had the fastest decomposition, losing 36% of its initial dry weight in 2 years. In contrast, western hemlock and Douglas-fir small roots were the most decomposition resistant, losing between 11% and 14% of their initial mass for the same period. For other class sizes, 10% or less of the initial mass was lost in 2 years. Woody root decomposition decreased with the increasing root size. Initial substrate quality indices could be used to predict the decomposition rate-constant (k) of fine and small roots. For all fine roots, lignin-cellulose index (LCI) and lignin-phenols:N together were the best predictor. Lignin:N ratio alone was the best predictor of k for coniferous fine roots. In small roots, the phenols:N ratio was the best predictor. Low temperature and high precipitation were the dominant limiting abiotic factors at Pringle Falls and Cascade Head site, respectively. Soil nitrogen availability had no direct influences on woody root decomposition despite a 5-fold difference between sites. Decomposing roots, especially fine roots, could be an important nitrogen source with as much as 70 Kg/ha/year of nitrogen released from dead roots after catastrophic disturbances (e.g., clear-cut, forest fire) in Douglas-fir old-growth forests.

3.2 INTRODUCTION

Roots are important structural and functional components of forested ecosystems (Grier et al., 1981; Harris et al., 1977, 1980; Hermann, 1977). A large amount of forest production is allocated to roots, similar in magnitude to foliage production (Harris et al., 1977; McClaugherty and Aber, 1982; Persson, 1979, 1980). This results in a large flux of carbon and nutrients into the belowground system (Cairns et al., 1997; Kurz et al., 1996; Vogt et al., 1986). Although tree root systems store large amounts of organic matter and nutrients in forest ecosystems, information on the rates and controls of root decomposition is scant, especially compared to the wealth of above ground litter decomposition data (Berg, 1984; Vogt et al., 1986; Waid, 1974). To better understand the nutrient cycling, soil organic matter dynamics, and carbon stores of forest ecosystems, more belowground root decomposition studies are needed.

Past studies on root dynamics have primarily focused on production and growth (Grier et al., 1981; McClaugherty and Aber, 1982; Persson, 1979, 1980). However, an understanding of root decomposition is important to properly estimate fine root production (Santantonio and Grace, 1987). The few root decomposition studies that have been conducted were carried out on fine roots in young forest stands, and were short-term (i.e., usually 1 year) (Camire et al., 1991). Moreover, the simple and less time consuming chronosequence approach was used more often than a time series (Fahey et al., 1988; Yavitt and Fahey, 1982) despite of its obvious disadvantages (Harmon et al., 1986). Experimental studies testing factors influencing root decomposition directly are even fewer in number, but critical to developing a predictive understanding of root decomposition (Berg, 1984; Camire et al., 1991; Waid, 1974).

Although the factors affecting root decomposition are generally known, the relative importance of biotic and abiotic factors and how these interact is poorly understood. The major biotic factors that may effect root decomposition include nitrogen, lignin, and carbon concentrations of the roots, the proportions of bark and wood, the decay organisms present, and their colonization patterns. So far the initial ratio of lignin to nitrogen concentration seems to be the best biotic predictor of root decomposition (Berg, 1984; Camire et al., 1991; Fogel and Cromack, 1977; McClaugherty et al., 1984, 1985). Abiotic factors with

the potential to influence root decomposition include temperature, moisture, oxygen concentration, and soil properties such as texture and nitrogen availability. Of these, temperature and moisture content are regarded as the main abiotic factors influencing root decomposition (Santantonio and Grace, 1987). Isolating the temperature and moisture effects on decomposition from other biotic factors is increasingly important if we are to understand the impact of climate change (Anderson, 1992).

Starting in June, 1995, I used litterbag techniques to measure the effects of root size and species on long-term decomposition at three locations: Cascade Head Experimental Forest (CAH), H. J. Andrews Experimental Forest (HJA), and Pringle Falls Experimental Forest (PRF). In this chapter, I analyzed the first 2.5 years of data from a 10 year experiment. Four questions important to the forests of the Pacific Northwest were addressed in this study.

1. How did the decomposition of woody roots vary with species?
2. How did root size influence root decomposition?
3. Could the decomposition rate-constants of woody roots be predicted from the root initial substrate quality indices such as lignin to nitrogen ratio?
4. How did the decomposition of woody roots vary under different climatic conditions?

3.3 STUDY SITES AND METHODS

3.3.1 Study sites

This decomposition time series study was conducted at Sitka spruce, Douglas-fir, and ponderosa pine dominated forests at CAH, HJA, and PRF, respectively. These three sites form a climatic gradient from warm and wet at CAH to cool and dry at PRF site. CAH is located on the Pacific coast near 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 high in organic matter and nitrogen. The dominant forest type is a mixture of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*),

although small stands dominated by Douglas-fir (*Pseudotsuga menziesii*) also occur. HJA is located 80 km east of 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 typic dystrochrepts; slope gradient ranges from 20-60%. The forests are classified into two major zones, the western hemlock zone (300-1550 m elevation) and the Pacific silver fir zone (1050-1550 m elevation). Douglas-fir and western redcedar (*Thuja plicata*) are also major components of both zones (Franklin and Dyrness, 1973). PRF is located in 57 km southwest of Bend, Oregon; east of the Cascades. The climate is modified continental, with a mean annual temperature of 5.7 °C and total 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 between 1310 and 1470 m. The forests are dominated by ponderosa pine (*Pinus ponderosa*) and lodgepole pine (*Pinus contorta*).

3.3.2 Methods

Experimental design. The overall experimental design for the root decomposition time series was a split-split plot with 3 sites, 4 plots within each site, 5 size classes, and 4 "backbone" species. Red alder (*Alnus rubra*), Douglas-fir, western hemlock, and ponderosa pine were the "backbone" species. The three incubation sites were CAH, HJA, and PRF. At each site, four plots were selected that were representative of the area's forest composition (Table 3-1). Plots were close each other, about 10 Km apart at the maximum distance and they had similar soil types. The 5 size classes included fine roots (< 2 mm diameter), small roots (2-10 mm), medium roots (10-50 mm), large roots (50-100 mm), and "jumbo" roots (> 100 mm). In addition, another 11 fine root, 4 small roots, and 3 medium roots species were included in the study (Table 3-2). Under the large and jumbo root categories, we only had lodgepole pine, ponderosa pine, and Douglas-fir. A total of 4500 root bags were buried at these 12 plots for a 10 year study.

Table 3-1. Characteristics of the study plots.

Site	Plot	Salvaged	Elevation (m)	Air Temp. (0^0C)[a]	Soil (20 cm) Temp. (0^0C)[a]	Precip. (mm)	Habitat type[b]
Cascade Head	1	No	233	8.70	9.94	3420	TSHE/PISI
	2	No	400	8.49	9.16	3420	TSHE/PISI
	3	No	266	8.63	9.86	3420	TSHE/PISI
	4	No	200	8.96	10.01	3420	TSHE/PISI
H. J. Andrews	1	No	1065	6.91	6.96	2290	TSHE/ABAM/RHMA /BENE
	2	No	935	7.51	7.61	2070	TSHE/RHMA/BENE
	3	Yes	535	7.88	7.97	2090	TSHE/RHMA/BENE
	4	No	865	7.68	7.56	2190	TSHE/RHMA/BENE
Pringle Falls	1	No	1400	6.03	6.87	525	PIPO
	2	Yes	1533	5.98	6.80	525	PIPO
	3	Yes	1766	4.66	5.17	525	PIPO
	4	Yes	1800	4.28	4.73	525	PIPO/PIMO/ABCO

[a] Based on December, 1995 - March, 1998 period.

[b] Based on the habitat types of Pacific Northwest forests.
Temp. = temperature and Precip. = precipitation.
TSHE/PISI = Tsuga heterophylla/Picea sitchensis.
TSHE/ABAM/RHMA/BENE=*Tsuga heterophylla/Abies amabalis/Rhododenron macrophyllum/Berberis nervosa.*
TSHE/RHMA/BENE = *Tsuga heterophylla/Rhododenron macrophyllum/ Berberis nervosa.*
PIPO = *Pinus ponderosa*.
PIPO/PIMO/ABCO = *Pinus ponderosa/Pinus monophylla/Abies concolor.*

Table 3-2. Harvesting history of root samples at the three sites*.

Roots/ Dowel	Genus_species	Code	Common_name	Incubation period (year)						
				0.25	0.5	0.75	1	1.5	2	2.5
Dowel	*Gonystylus bancanus*	GOBA	Ramin	X	X	X	X	X	X	X
Fine	*Pinus ponderosa*	PIPO	ponderosa pine	X	X	X	X	X	X	X
roots	*Pseudotsuga menziesii*	PSME	Douglas-fir	X	X	X	X	X	X	X
	Tsuga heterophylla	TSHE	western hemlock	X	X	X	X	X	X	X
	Alnus rubra	ALRU	red alder	X	X	X	X		X	X
	Acer macrophyllum	ACMA	bigleaf maple		X		X		X	
	Abies magnifica	ABMA	California red-fir		X		X		X	
	Calocedrus decurrens	CADE	incense-cedar		X		X		X	
	Fraxinus latifolia	FRLA	Oregon ash		X		X		X	
	Picea engelmanni	PIEN	Engelmann spruce		X		X		X	
	Pinus contorta	PICO	lodgepole pine		X		X		X	
	Pinus monophylla	PIMO	nut pine		X		X		X	
	Thuja plicata	THPL	western redcedar		X		X		X	
	Abies concolor	ABCO	white fir				X		X	
	Abies procera	ABPR	noble fir				X		X	
	Acer rubrum	ACRU	red maple				X		X	
Small	*Pinus ponderosa*	PIPO	ponderosa pine				X		X	
roots	*Pseudotsuga menziesii*	PSME	Douglas-fir				X		X	
	Purshina tridentata	PUTR	antelope-brush				X		X	
	Tsuga heterophylla	TSHE	western hemlock				X		X	
	Alnus rubra	ALRU	red alder						X	
	Castanopsis chrysophylla	CACH	golden chinkapin						X	
	Calocedrus decurrens	CADE	incense-cedar						X	
	Rhododendron-macrophyllum	RHMA	Pacific rhododendron						X	
Mediun	*Alnus rubra*	ALRU	red alder				X		X	
roots	*Pinus contorta*	PICO	lodgepole pine				X		X	
	Pinus ponderosa	PIPO	ponderosa pine				X		X	
	Pseudotsuga menziesii	PSME	Douglas-fir				X		X	
	Tsuga heterophylla	TSHE	western hemlock				X		X	
Large	*Pinus contorta*	PICO	lodgepole pine				X		X	
roots	*Pinus ponderosa*	PIPO	ponderosa pine				X		X	
	Pseudotsuga menziesii	PSME	Douglas-fir				X		X	
Jumbo	*Pinus contorta*	PICO	lodgepole pine						X	
roots	*Pinus ponderosa*	PIPO	ponderosa pine				X		X	

*: Fine roots: 0-2 mm; Small roots 2-10 mm; Medium roots 10-50 mm; Large roots 50-100 mm; Jumbo roots > 100 mm.

X indicates the incubating root samples were harvested.

Fine roots. Of 15 species examined, 11 were coniferous and 4 were deciduous species. All the species are common in the Pacific Northwest. The 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. After the fine roots (< 2 mm) were trimmed from seedlings, they were transported to Corvallis, Oregon where they were cleaned by rinsing with tap water and then spread on trays and air-dried at 15 to 20 ^{0}C room temperature to a constant mass (≅ 10 days). Air-dry moisture contents of fine roots ranged from 6.0 to 9.5 % across the species, but the variations were < 0.5% within each species. Approximately 10 g amounts of air-dry fine roots were weighed and put into 20 x 20 cm dacron cloth litterbags with an effective mesh size of 50 μm. This design was used to contain the fine particulate matter created by the fine root decomposition. Each litterbag was tagged with a unique numbered aluminum tag. Subsamples were retained for initial moisture, ash, and chemical analyses.

Small, medium, large, and jumbo roots. Small-, to, jumbo-sized roots were collected from recently uprooted trees caused by wind or road building near the three sites. These woody roots were cleared of surface soil first, then sorted into small (2-10 mm), medium (10-50 mm), large (50-100 mm), and jumbo diameter classes (>100 mm). They were cut into 20 cm long segments then air-dried at 15 to 20 ^{0}C room temperature to a constant mass (20-50 days). Air-dry moisture contents of small roots ranged from 7 to 10.3 % across the species, but the variations were < 0.5% within each species. Approximately 10 g amounts of air-dry small roots were weighed and placed into 20 x 20 cm dacron cloth litter bags similar to those used in fine roots.

Due to the wide variation of moisture content in medium, large, and jumbo roots, we determined the moisture content of each root segment by removing subsamples from each root. Total dry weight of each root segment was determined by the total air-dried weight and its moisture content. The ends of each segment was sealed using neoprene paint to prevent end rot before putting it into a nylon mesh bag (mesh size = 0.4 mm). One root segment was placed into each mesh bag. The size of each mesh bag varied with the root sample. Each litterbag of root sample was tagged

by a unique numbered aluminum tag. Subsamples of each species of different size roots were retained for initial ash and chemical analyses.

The proportions of structural components of root samples were measured prior to field incubation. The structural components of woody roots include outer bark, inner bark, wood, and resin cores. The latter are analogous to knots in bole and branch wood. In general, resin cores did not occur in these root samples because we tried to avoid them when we collected fresh root samples in fields. Each size class of roots, 5-10 root segments were randomly chosen for the measurement. The single-side thickness of outer bark and inner bark of each root was recorded in addition to the outmost diameter of root segments. Three measurements were taken on each root examined.

Root placement. 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 top 20 cm soil at each plot randomly. We planned to retrieve root samples 15 times during a 10 year experiment. Root samples were placed in the field in June of 1995.

Dowel incubation. To compare the favorability of root decomposition at the three sites, 15 dowels were installed at each plot when root samples were buried. Each dowel was placed vertically so that half of the dowel was above- and half was belowground. The belowground part of the dowel was covered by mesh sleeve (size = 0.4 mm). Dowels were 1 cm in diameter, 61 cm long, and composed of *Gonystylus bancanus*, a non-decay-resistant tropical tree species.

Harvest of decomposing roots and dowel. Root samples are to be harvested in different time intervals during the 10 year experiment (Table 3-2). Fine roots of the "backbone" species will be harvested 14 times, whereas the other 11 species will be harvested 4-6 times over 10 year period. Small and medium roots will be sampled for 6 - 10 times during 10 year study. Most large roots will be harvested annually and jumbo roots will be harvested 5 times for the same period. Thus far the fine roots of "backbone" species have been harvested 7 times and small roots twice. During harvest each root litterbag was placed into a ziplog plastic bag on site to prevent moisture loss after retrieving from soils. Later the moisture content of root samples was calculated

from the wet weight and oven dry weight of the root sample. One buried dowel was retrieved for each root harvest. Each harvested dowel was cut into aboveground and belowground portions and put into two separate plastic bags for laboratory analysis.

Decomposition rates of roots and dowels. Decomposition rates of woody roots were estimated from changes in ash free dry weight mass of roots. After recovery, root and dowel samples were returned to 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. If the roots were large, the roots were chopped into smaller piece before drying. The length of aboveground and belowground portions of dowels was measured. Weight losses from roots and dowels were calculated after correcting for ash content. 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.

Soil nitrogen availability. Soil nitrogen availability of three sites was measured by ion exchange resin bags (Binkley, 1984; Binkley and Matson, 1983). This method has proved a simple measure of in-field nitrogen availability that is relevant to ecosystem nutrient cycling and production (Binkley, 1984; Binkley and Matson, 1983). Resin bags were prepared by placing mixed-bed ion-exchange resin (J. T. Baker catalog no. 4631-1) in nylon stockings (Binkley and Matson, 1983). Each bag contained 30 g moist weight of resin (equivalent to about 16.5 g dry weight) with anion and cation exchange capacities of 2.6 meq/g. At each site where roots were placed we buried 10 resin bags which were connected by a nylon line in the top 20 cm soil during June of 1995. These resin bags were collected one year later and air dried. Finally, we analyzed ammonium and nitrate concentrations of each resin sample. Four to 5 g dry resin of each resin sample was extracted with 50 ml of 1 M KCl. Ammonium and nitrate were determined by automated solution chemistry procedures (McClaugherty et al., 1985). Extracts of resin blanks had no detectable ammonium or nitrate. Soil nitrogen availability was expressed by index of ammonium, nitrate or their summation.

Near Infrared Reflectance Spectroscopy (NIRS). All the samples were scanned using a NIRS (Near Infrared Reflectance Spectroscopy) Systems 6500

analyzer to predict their ash and N concentrations. A calibration is required to known chemical concentrations from laboratory analyses. The NIRS ash calibration was conducted on the entire sample set from the three sites. About 16.8% (146) of the root samples were randomly selected out of total 868 root samples to provide for ash and nitrogen calibration. These root samples were analyzed for ash concentration using a muffle furnace and nitrogen content by the micro-Kjeldahl technique (see below). The equations developed from these calibrations were then used to predict ash and N concentration of root samples that had been scanned. All the mass, carbon, and nitrogen values reported in this paper are ash-free values.

Wet chemistry analyses. We analyzed ash, carbon, and nitrogen concentrations of the selected root samples at the Soils Laboratory of Forest Science, Oregon State University. Ash content was determined by heating in a muffle furnace at 500 °C for 4 hours. The total organic carbon of most samples was approximately estimated from ash data (Allen et al., 1974). The organic carbon formula can be expressed as follows:

Carbon % = (100-ash%)/Conversion factor

where the conversion factor was obtained from the C-N analyzer. The conversion factor for decomposing root bark and root wood is 1.87 (se = 0.16, n = 24) and 1.93 (se = 0.18, n = 24), respectively; while the factor for whole roots is 1.90 (se = 0.17, n = 48).

Nitrogen was measured either by the micro-Kjeldahl technique, with the digestate analyzed by automated solution chemistry procedures (Alpkem Rapid Flow Analyzer 300 series) (McClaugherty et al., 1985), or by Carlo-Erba C-N analyzer. Cross-laboratory comparisons have shown that these two techniques are equivalent (Glassman, personal communication 1997; McLellan et al., 1991a). In this study,nitrogen concentration of 121 root samples was analyzed by Kjeldahl technique and 47 root samples were measured by Carlo-Erba C-N analyzer.

The organic constituents of all species and size roots in the time series study were analyzed by proximate analysis to determine initial substrate quality. Considering the effort required for these chemical methods, replicate analyses were not done.

Instead of one standard pine needle sample with known initial substrate quality was included at each batch to assure quality control. The constituents analyzed included nonpolar extractives (NPE: fats, oils, and waxes) using dichloromethane as the extratant (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-soluble carbohydrates (cellulose, hemicellulose, and starch, hydrolysis followed by the phenol-sulfuric acid assay, DuBois et al., 1956), and acid-insoluble carbon (Effland, 1977). Although the acid-insoluble fraction includes other recalcitrant carbon fraction besides lignin (e.g., suberin), we will simply refer to this as "lignin".

Measurement of microclimate. Soil microclimate data were collected at each plot from September of 1995. We measured the soil temperature at 20, 40, and 60 cm depths as well as air temperature (1 m high) using thermisters (YSI 44006 from Yellow Springs). Air and soil temperatures were recorded hourly and every 12 hours, respectively. Gypsum blocks (w/o blocking capacitors item #223 from Campbell Scientific Inc.) were installed to provide qualitative soil moisture data at the same depths that soil temperatures were measured. Soil moisture data was recorded every 12 hours. Time Domain Reflectometry (TDR) (Fritschen and Gay, 1979) was used to measure the volumetric soil moisture of the same three soil depths at each plot once every three months.

3.3.3 Statistical analysis

Analysis of variance with a split-split-plot experimental design was used to test the effects of site, species, root size, and their interactions upon mass loss of roots. The same approach was also employed to test the effects of site, dowel position (above- versus belowground), and their interactions upon the mass loss of dowels.

Decomposition rate-constants (k) of roots were calculated by two methods. For the 4 backbone fine roots and dowels we had at least 6 sampling times (Table 3-2). The exponential decomposition rate-constants of these roots were calculated using regression analysis. The regression equation used was:

$$\ln Y_t = \ln Y_0 - k * t$$

where Y_0 is the initial dry mass of fine roots or dowel, Y_t is the amount left at time t, and k is the decomposition rate-constant. For the other roots we only had three or two sample times, therefore we computed the decomposition rate-constant from the following equation based on the last harvest:

$$-k = [\ln (Y_t / Y_0)]/t$$

where Y_t is the remaining mass of last time (t) harvest and is Y_0 the initial mass. The half-life ($T_{0.5}$) was calculated from the decomposition rate-constant:

$$T_{0.5} = 0.693/k$$

where k is the decomposition rate-constant.

Effects of initial root substrate quality on the decomposition rate-constant of roots were evaluated using regressions. A simple linear regression was developed with decomposition rate-constants as the dependent variable and each initial root quality index as the independent variables. The effect of the initial substrate quality index on decomposition rate-constant was evaluated based on the P value of the model. Finally multiple-linear regressions using a stepwise procedure was applied to determine the final model. Fine roots were first treated as one group and then divided into fine roots from coniferous versus deciduous trees. Due to the limited number of species in the medium, large, and jumbo size classes, these roots were combined into one group for analysis purposes. Indices of initial root quality in these analyses included initial concentrations of all the organic fractions as well as N, C, C:N, and lignin:N.

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

3.4 RESULTS

3.4.1 NIRS prediction of ash and nitrogen concentrations

The determination coefficients (R^2) of ash and nitrogen of decomposing root samples were 0.98 and 0.99 ($P = 0.0001$) respectively. These calibration results were as good as previous reports (Bolster et al., 1996; Joffre et al., 1992; Mclellan et al.,

1991a, 1991b; Wessman et al., 1988; Winch and Major, 1981). In contrast, the predictions of ash and nitrogen for dowels were poorer than for roots with a determination coefficient (R^2) of ash and nitrogen 0.94 ($P = 0.001$) and 0.95 ($P = 0.001$), respectively. Graphic comparisons between values predicted with NIRS calibration equations and those obtained by wet chemical analyses (Figure 3-1) indicated NIRS could successfully determine ash and nitrogen concentration of woody roots as well as foliage litter (Joffre et al., 1992; McLellan et al., 1991a, 1991b; Wessman et al., 1988).

3.4.2 Decomposition

3.4.2.1 Dowels

Belowground dowels decomposed faster than the aboveground dowels at all three sites during the first two and half years, although the difference between them was not significant ($P > 0.05$) (Figure 3-2). At CAH, the aboveground dowels lost 11.6% of initial mass, while the belowground dowels lost 23.6% of initial mass in 2.5 years. For the same period, the aboveground dowels and belowground dowels lost 8.5% and 26.3% at HJA and 4.2% and 30.8% at PRF, respectively. The differences in the mass loss of aboveground and belowground dowel increased gradually with the incubation time at all three sites (Figure 3-2).

Split-split ANOVA analysis indicated that no significant site effects ($P > 0.05$) were observed on the decomposition of above- and belowground portions of dowel after 1, 2, and 2.5 years of decomposition, a result that was quite different from that we expected (Figure 3-3). We hypothesized that the dowels at CAH or HJA would decompose faster than PRF because the annual temperature of the former two sites was higher than PRF. Comparing the decomposition of belowground dowels from three sites we found the belowground dowel of PRF showed the fastest decomposition, HJA the second, and CAH the slowest after 2 or 2.5 year of decomposition, although the differences were not significant ($P > 0.05$). However, the decomposition pattern of aboveground dowels of three sites was the opposite to the belowground dowels, with

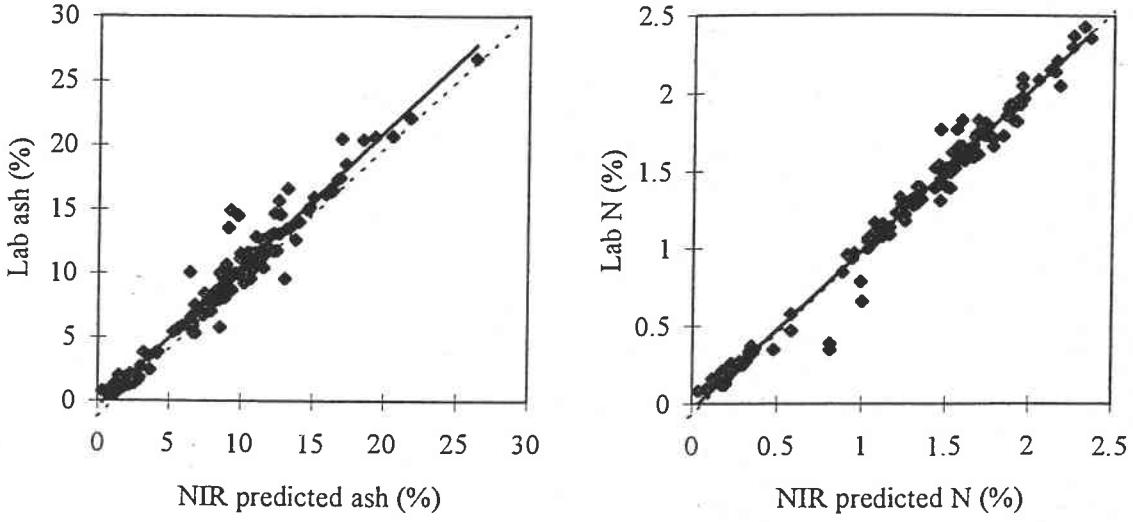

Figure 3-1. Relationship between NIR predicted values and wet chemistry values (% of dry matter)*.

* dashed line is a 1:1 line and solid line is a regression line. CAH, HJA, and PRF refer to Cascade Head, H.J. Andrews, and Pringle Falls site, respectively.

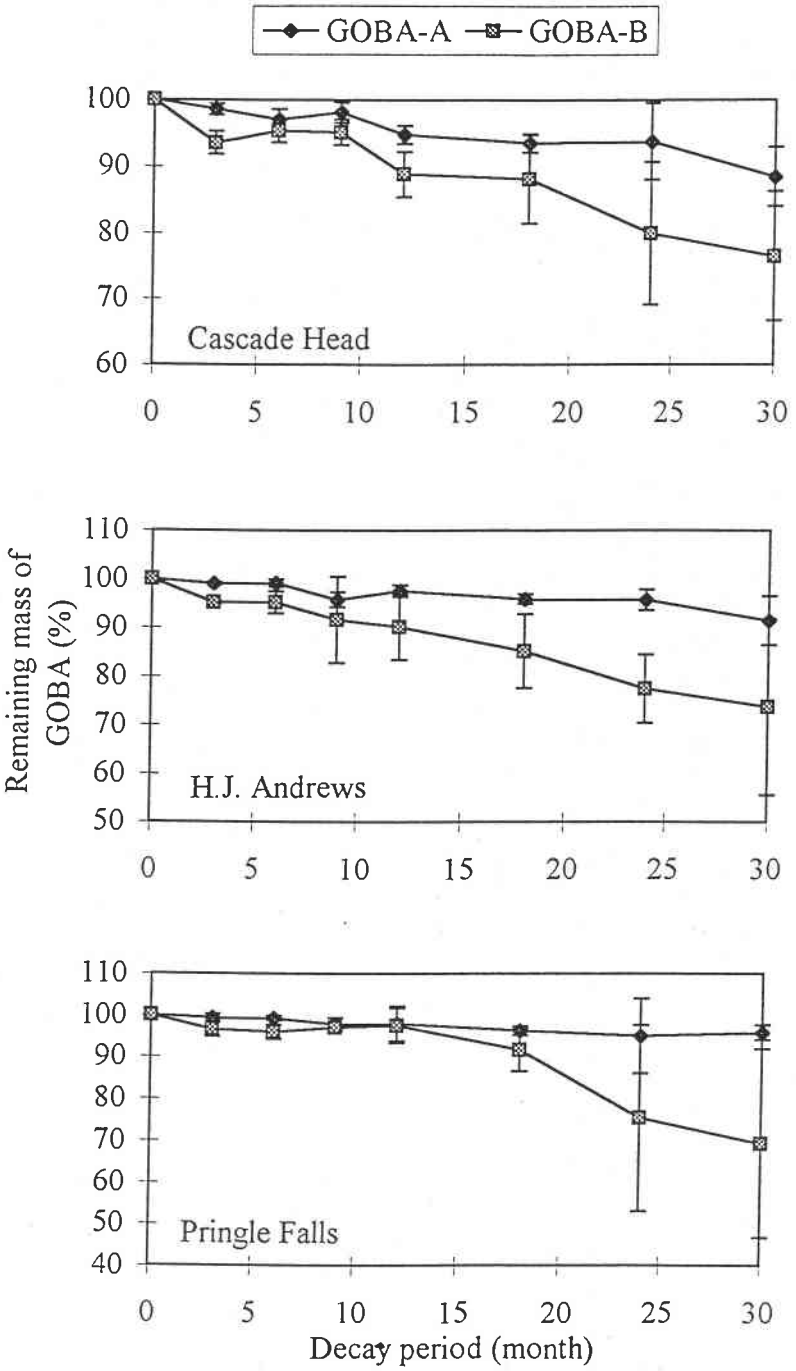

Figure 3-2. Dowel mass loss over time at three sites*.

*: A, aboveground dowel; and B, belowground dowel.

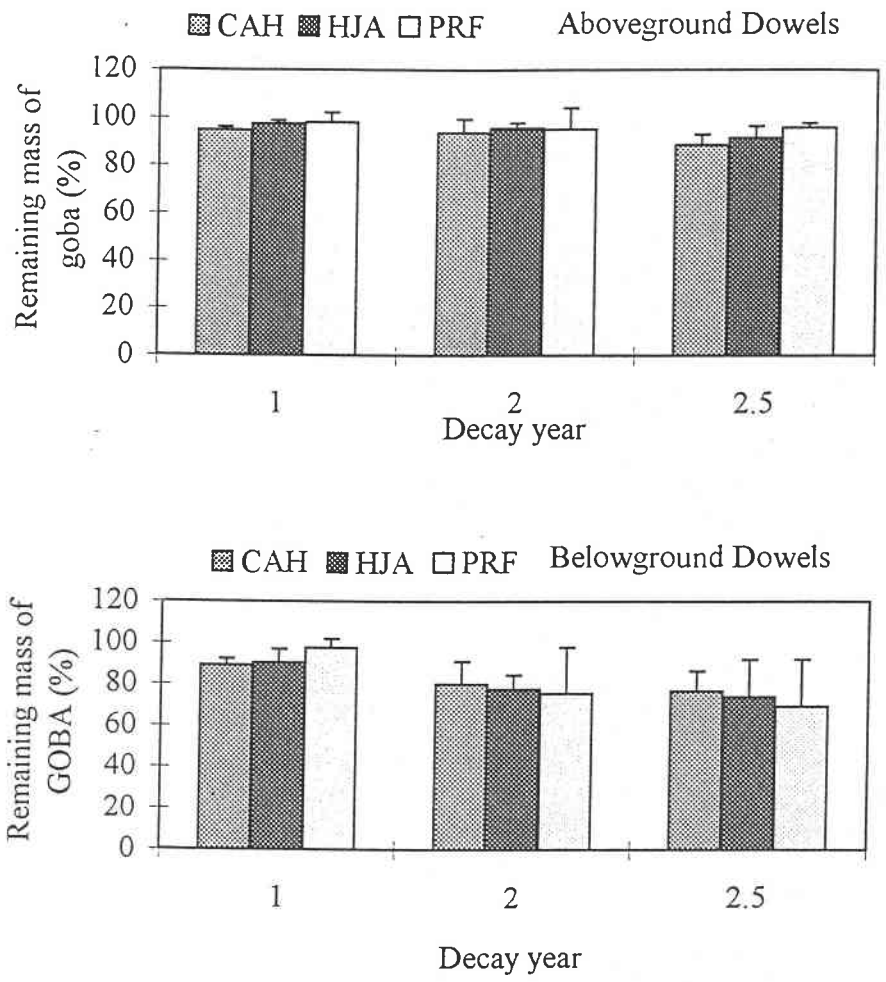

Figure 3-3. Decomposition of aboveground and belowground dowels at three sites*.

* CAH, HJA, and PRF refer to Cascade Head, H.J. Andrews, and Pringle Falls site, respectively.

CAH the fastest, HJA the second, and PRF the slowest after 2.5 years of decomposition.

3.4.2.2 Roots

3.4.2.2.1 Fine roots

Split-split plot ANOVA analysis showed that no significant differences ($P > 0.05$) were observed in the decomposition of the 4 "backbone" fine roots among the three sites. In contrast, species appeared to significantly ($P < 0.05$) influence the decomposition of fine roots during the first 2.5 years of decomposition, except for the 5th and 7th harvests (Table 3-3). Red alder decomposed faster than Douglas-fir, western hemlock, and ponderosa pine which all showed very similar decomposition patterns to each other (Figure 3-4). The interaction of species and site was not significant at any time (Table 3-3). The other 11 species showed significant differences in mass loss during the first year of decomposition, although species effects were not significant for the 2 year data. As we observed in the decomposition of "backbone" species, the site effect was not significant (Table 3-4). The lack of species effect after 2 years suggests a decreasing role of species related factors on fine roots with time.

Fine roots showed a rapid loss of mass during the first 3 to 6 months, with a dramatic slowing thereafter (Figure 3-4). 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 quarter of their mass over the same time period. During 2 years of decomposition red alder cumulatively lost about 62% of its initial mass. The mass loss curves of Douglas-fir, western hemlock, and ponderosa pine were very similar to each other (Figure 3-4) losing about 40% of the initial mass after 2 years (Table 3-5). Similar temporal patterns were observed in the fine root decomposition of the other 11 species, although we were not sure when during the first 6 months this quick mass loss occurred (Figure 3-4). Of the 11 examined species, Oregon ash had the fastest decomposition, losing 42.3%, 45.2%, and 42.6% of initial mass at CAH, HJA, and PRF, respectively, in the first 6 months; while incense-cedar, the slowest in our study,

Table 3-3. Split-split ANOVA results for "backbone" species fine root decomposition at each harvest date expressed as % initial mass remaining.

Harvest	Source	Error term	F ratio	df	P value
1 (3 mo)	Site	rep(site)	0.89	2, 47	0.50
	Species	species x rep(site)	12.67	3, 47	0.00
	Species X Site	species X rep(site)	0.29	6, 47	0.93
2 (6 mo)	Site	rep(site)	0.05	2, 47	0.95
	Species	species x rep(site)	3.92	3, 47	0.05
	Species X Site	species X rep(site)	0.55	6, 47	0.76
3 (9 mo)	Site	rep(site)	5.10	2, 47	0.11
	Species	species x rep(site)	3.61	3. 47	0.06
	Species X Site	species X rep(site)	0.73	6, 47	0.64
4 (12 mo)	Site	rep(site)	0.05	2, 47	0.95
	Species	species x rep(site)	4.83	3, 47	0.03
	Species X Site	species X rep(site)	0.71	6, 47	0.65
5 (18 mo)	Site	rep(site)	0.36	2, 35	0.72
	Species	species x rep(site)	2.59	2, 35	0.15
	Species X Site	species X rep(site)	2.46	4, 35	0.16
6 (24 mo)	Site	rep(site)	0.87	2, 47	0.50
	Species	species x rep(site)	3.90	3, 47	0.05
	Species X Site	species X rep(site)	1.10	6, 47	0.43
7 (30 mo)	Site	rep(site)	1.75	2, 35	0.31
	Species	species x rep(site)	2.18	2, 35	0.19
	Species X Site	species X rep(site)	1.04	4, 35	0.46

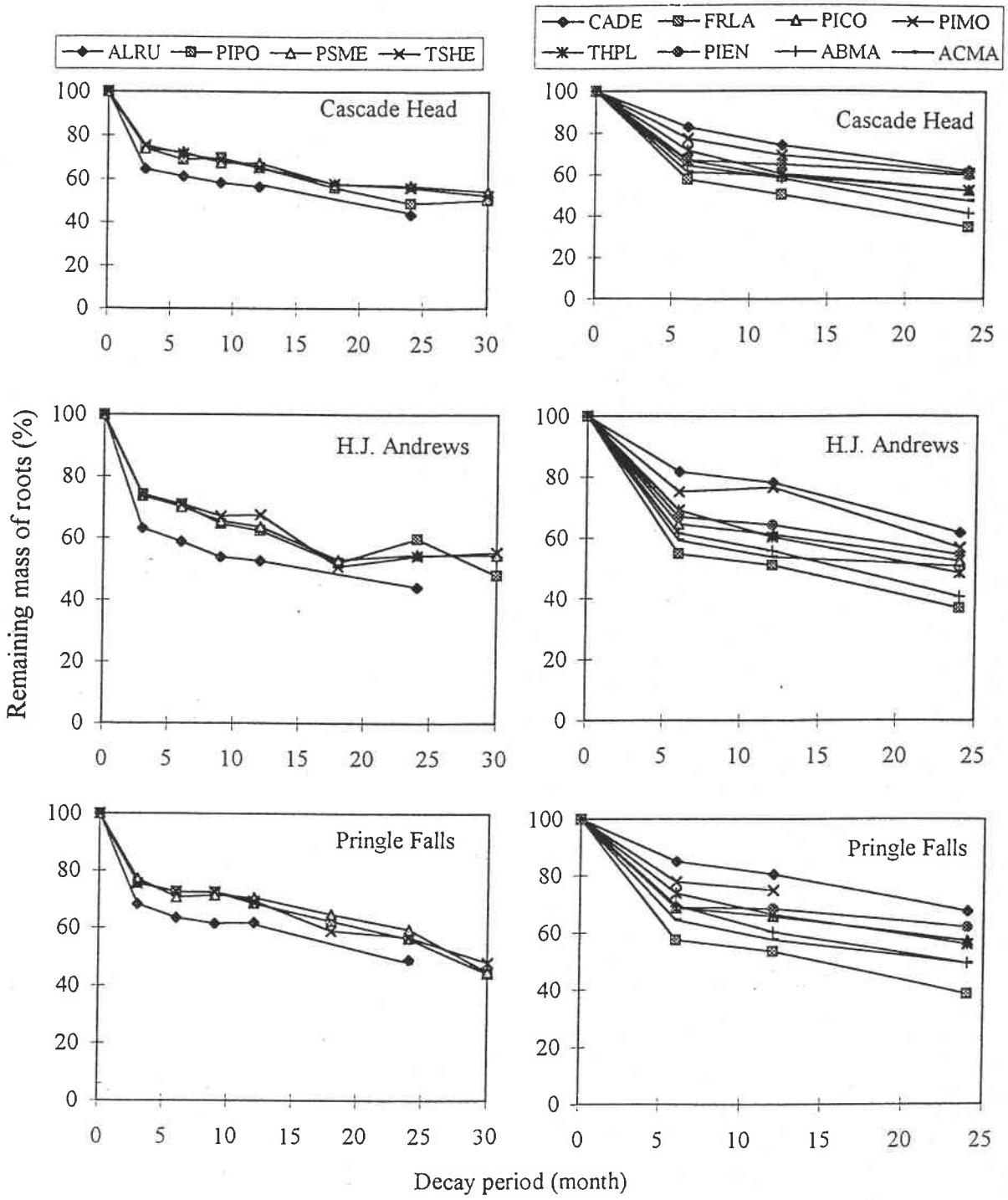

Figure 3-4. Fine root decomposition at three sites.

Table 3-4. Split-split ANOVA results for fine (non-backbone species), small, medium, large, and jumbo root decomposition comparing site and species effects.

Root type	Source	Error term	Harvest 4 (12 mo)			Harvest 6 (24 mo)		
			F ratio	df	*P* value	F ratio	df	*P* value
Fine	Site	rep(site)	0.1	2, 131	0.90	0.7	2, 125	0.57
	Species	Species x rep(site)	5.9	10, 131	**0.00**	1.3	10, 125	0.28
	Species X Site	Species x rep(site)	1.0	20, 131	0.50	0.9	20, 125	0.63
Small	Site	rep(site)	1.1	2, 47	0.44	0.8	2, 115	0.52
	Species	Species x rep(site)	11.2	3, 47	**0.00**	2.7	7, 115	**0.04**
	Species X Site	Species x rep(site)	0.7	6, 47	0.68	1.1	13, 115	0.41
Medium	Site	rep(site)	5.0	2, 59	0.11	1.1	2, 71	0.44
	Species	Species x rep(site)	6.7	4, 59	**0.00**	2.7	4, 71	0.08
	Species X Site	Species x rep(site)	1.3	8, 59	0.35	1.4	8, 71	0.31
Large	Site	rep(site)	1.4	2, 35	0.37	1.6	2, 35	0.34
	Species	Species x rep(site)	1.0	2, 35	0.42	2.8	2, 35	0.14
	Species X Site	Species x rep(site)	0.5	4, 35	0.77	0.5	4, 35	0.73
Jumbo	Site	rep(site)				1.0	2, 21	0.46
	Species	Species x rep(site)				1.9	1, 21	0.26
	Species X Site	Species x rep(site)				13.9	2, 21	0.03

Table 3-5. Mass loss of different size woody roots during 2 years of decomposition at three sites*.

Root Type	Species	Cascade Head		H.J. Andrews		Pringle Falls	
		mean	se	mean	se	mean	se
Fine roots	Oregon ash	65.1	4.5	63.1	2.3	61.4	4.5
	California red-fir	58.5	9.2	59.3	9.8	50.7	6.1
	red alder	56.4	4.2	56.0	4.9	51.0	9.2
	white fir	53.1	2.8	55.6	10.0	47.5	5.9
	bigleaf maple	52.5	3.9	49.3	8.9	50.7	6.0
	red maple	49.7	2.3	53.5	3.3	48.7	6.9
	lodgepole pine	47.4	1.2	47.7	5.5	43.0	13.1
	western redcedar	47.3	3.9	51.5	0.7	44.2	4.7
	noble fir	46.8	2.8	55.2	19.4	44.0	3.9
	ponderosa pine	43.9	1.7	40.3	7.2	43.7	8.5
	Douglas-fir	42.4	5.9	45.4	10.7	40.5	2.2
	western hemlock	42.1	3.4	45.9	4.6	43.1	5.1
	Engelmann spruce	40.1	10.6	45.6	18.7	38.2	3.5
	nut pine	39.1	4.7	43.1	17.1	33.3	4.7
	incense-cedar	37.9	3.0	38.3	6.9	32.6	8.2
Small roots	antelope-brush	37.1	13.3	14.6	0.6	18.8	7.1
	ponderosa pine	32.8	5.8	39.9	16.1	36.1	3.6
	golden chinkapin	24.8	4.1	20.2	6.5	39.1	32.7
	incense-cedar	19.9	6.1	19.2	4.9	17.8	7.4
	Pacific rhododendron	19.6	1.4	30.2	12.5	na	na
	red alder	14.7	5.0	32.4	22.5	24.3	23.3
	Douglas-fir	13.0	5.8	13.3	1.2	15.4	4.7
	western hemlock	11.0	1.7	11.1	7.2	11.1	3.7
Medium roots	red alder	12.8	6.6	13.6	9.5	na	na
	ponderosa pine	12.5	5.8	10.0	9.1	6.0	2.9
	western hemlock	9.6	4.7	7.2	7.4	5.8	1.7
	lodgepole pine	9.0	1.3	9.9	10.1	10.9	6.3
	Douglas-fir	7.7	0.9	12.2	2.1	11.7	6.2
Large roots	Douglas-fir	12.8	6.6	14.6	3.2	8.3	7.6
	lodgepole pine	11.0	3.9	7.8	9.1	14.2	3.8
	ponderosa pine	2.9	2.6	3.1	3.1	9.5	9.7
Jumbo roots	ponderosa pine	7.8	5.0	5.2	9.9	2.4	3.3
	lodgepole pine	1.3	2.3	5.3	1.3	5.6	5.2

*: mean and stardard error (se) were based on 4 samples.
na, not available.

only losing 17.1%, 18.3%, and 14.9% at CAH, HJA, and PRF, respectively, during the same period. At the end of 2 years of decomposition, Oregon ash still decomposed the fastest losing 61.4 - 65.1% of its initial mass, whereas incense-cedar, continued to be the slowest decomposing species, only losing 32.6 - 38.3% of the initial mass (Table 3-5 and Figure 3-4).

In general, the fine roots of deciduous species decomposed faster than those of coniferous species (Table 3-5). At CAH, Oregon ash, red alder, red maple, and bigleaf maple, the four deciduous species were among the 6 fastest decomposing species of all 15 species after 2 years of decomposition. At HJA, these deciduous species (except bigleaf maple) were also among the 6 fastest decomposing species. Similarly, they were ranked in the 5 fastest decomposing species at PRF for the same time period. For deciduous species, no obvious differences in mass loss were observed after 1 or 2 years of decomposition. However, significant differences ($P = 0.011$) were detected among 11 coniferous species after 1 year decomposition, although a similar pattern did not occur one year later.

3.4.2.2.2 Small roots

Species appeared to significantly influence mass loss of small roots during first two years of decomposition but the impact of sites was not significant on small root decomposition (Table 3-4 and Figure 3-5). Ponderosa pine decomposed the fastest in the first year of decomposition at all three sites (Figure 3-5). At the end of the 2 year incubation period, antelope-brush was the fastest decomposing species among 8 species at CAH, losing 37% of its initial mass; and ponderosa pine was the second, losing about 33% of its initial mass (Table 3-5). At HJA, ponderosa pine was ranked the fastest decomposing species, losing about 40% of initial mass; and red alder the second, losing about 32%. A similar pattern was observed at PRF where golden chinkapin and ponderosa pine were the two fastest decomposing species, losing about 39% and 36% of their original mass. Western hemlock and Douglas-fir were the most decomposition resistant species, losing about 11% and 13-15% of initial mass during 2 years, regardless of site (Table 3-5).

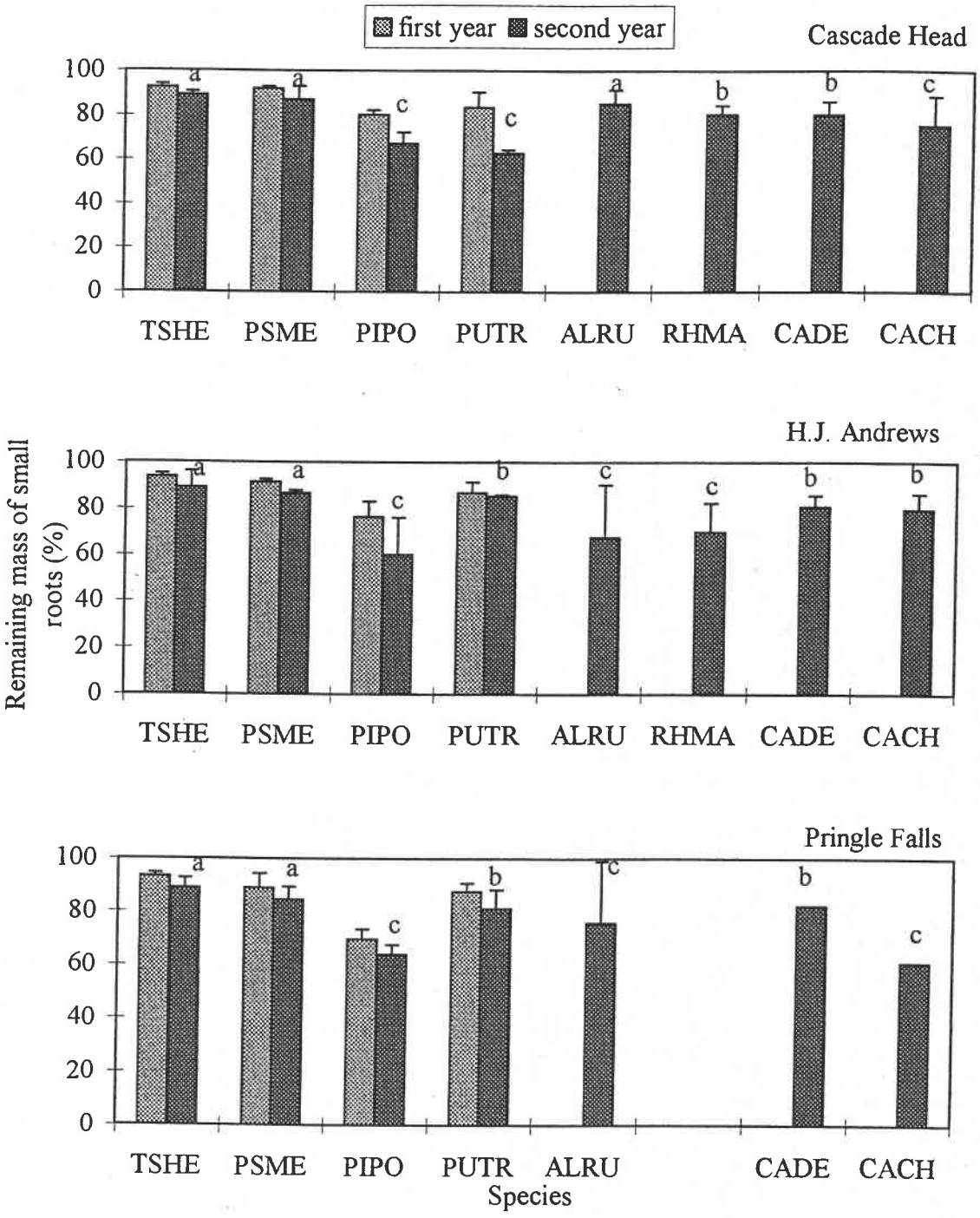

Figure 3-5. Decomposition of small roots at three sites*.

* Different letter in each bar indicates significantly different ($P < 0.05$).

3.4.2.2.3 Medium, large, and jumbo roots

Neither site nor species had significant effects on the decomposition of medium, large, and jumbo woody roots, except that species showed significant influence after the first year decomposition of medium roots (Table 3-4). For medium roots, red alder was the fastest species at CAH and HJA, losing about 12.8% and 13.6% respectively of its initial mass during 2 years of decomposition, although most species lost 10% or less of their initial mass in a 2 year period (Figure 3-6). For large roots, roughly 10% of initial mass was decomposed by 2 years, an amount that was very close to the losses of medium roots. Only about 5% of initial mass of jumbo roots was lost after 2 years (Figure 3-6) which is consistent with the idea that larger diameter woody roots require more time for fungal colonization.

3.4.2.3 Decomposition rate-constant (*k*)

3.4.2.3.1 Fine roots

Differences in fine root decomposition rate-constants of the same species among three sites were not obvious, although in most species the *k* of fine roots was slightly higher at HJA or CAH than PRF (Figure 3-7). This trend was consistent with the mass loss of fine roots which was not significantly influenced by sites (Table 3-3). However, site effects on fine root decomposition still appeared to exist. For example, the slowest decomposition rate-constants of red alder, ponderosa pine, Douglas-fir, and western hemlock always appeared in PRF and the fastest decomposition rate-constants of Douglas-fir and western hemlock occurred in HJA (Figure 3-7a). For red alder and ponderosa pine, the fastest k appeared in CAH. A similar pattern recurred for the other 11 species. Of these, 8 species had the fastest *k* of fine roots at HJA and 3 species (Oregon ash, bigleaf maple, and Engelmann spruce) showed their fastest *k* at CAH (Figure 3-7b). In contrast, 9 species exhibited the slowest decomposition rate-constant at PRF.

Species varied in their *k* when averaged for the three sites. Of the 4 "backbone" species, the order of increasing *k* calculated from the regressions was Douglas-fir <

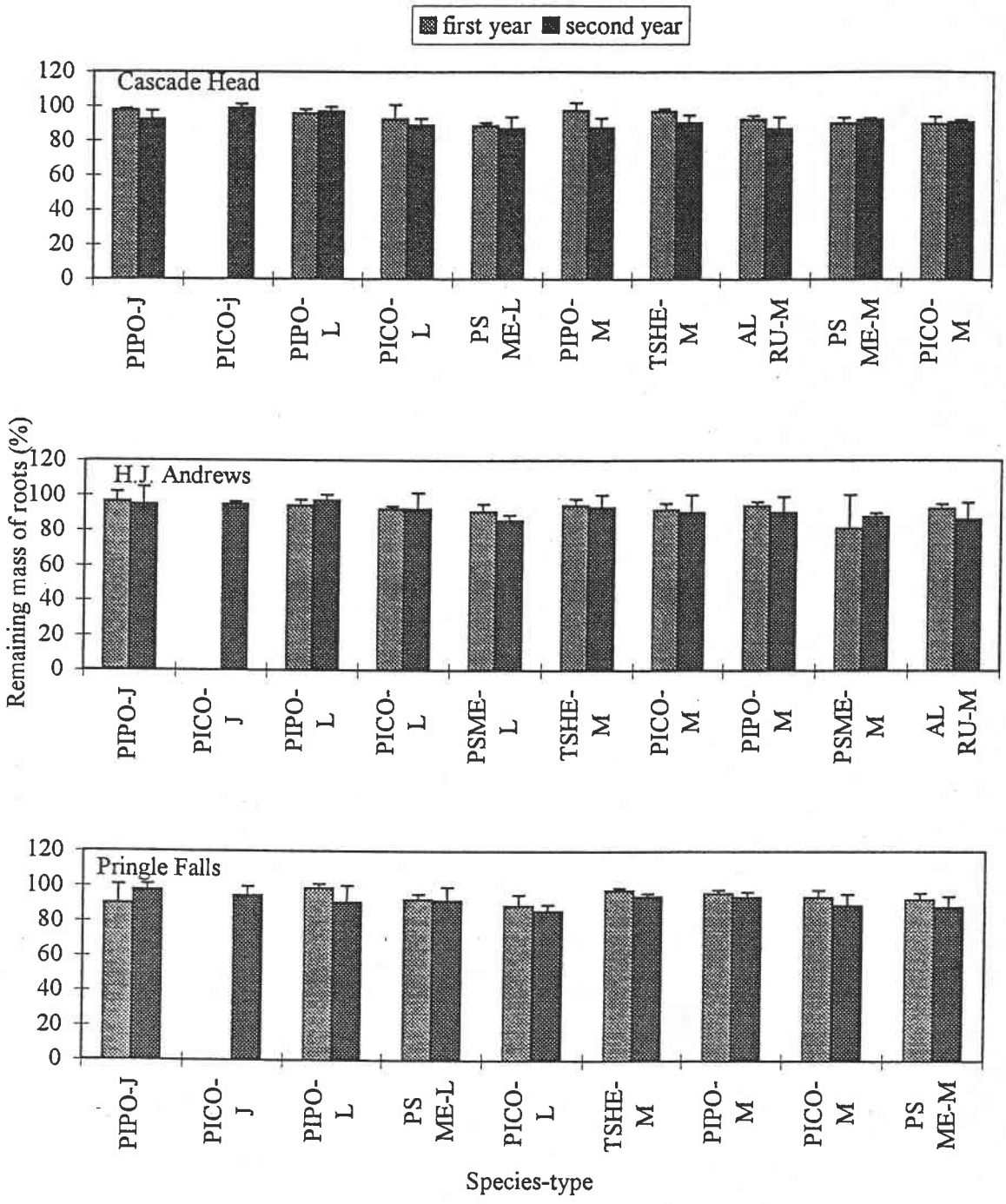

Figure 3-6. Decomposition of medium (M), large (L), and jumbo (J) roots at three sites.

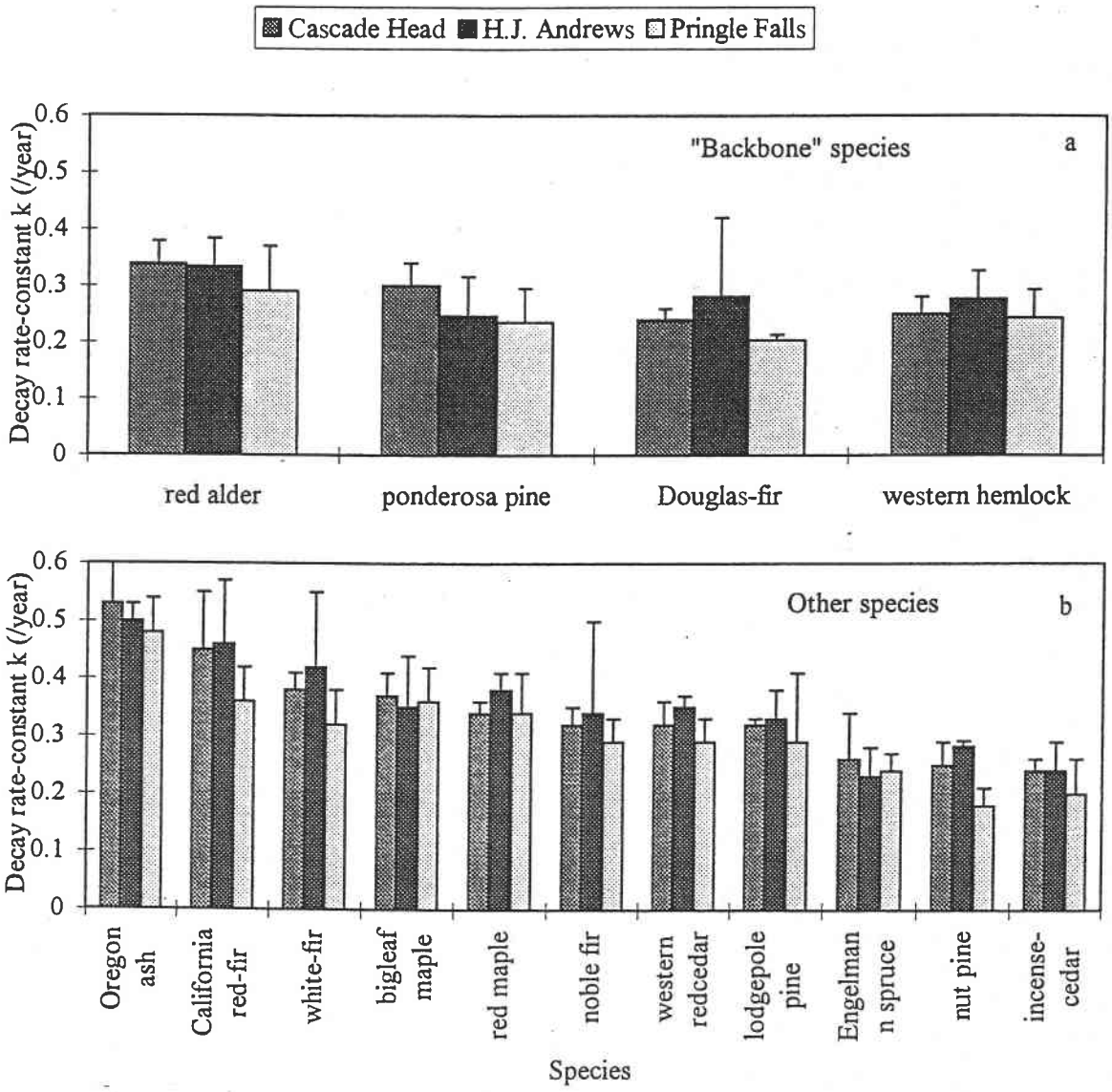

Figure 3-7. Decomposition rate-constants of fine roots at three sites.

western hemlock < ponderosa pine < red alder. For other 11 species, the order of fine root *k* was incense-cedar < nut pine < Engelmann spruce < lodgepole pine < noble fir < western redcedar < red maple < bigleaf maple < white fir < California red-fir < Oregon ash (Table 3-6). Among these 15 species (comparing the decomposition rate-constant based on the one-harvest time approach), the fastest decomposing fine root was Oregon ash with a half-life of 1.4 years; the second fastest species was California red-fir; whereas the slowest decomposing species was incense-cedar with a decomposition rate less than half of that of Oregon ash.

Decomposition rate-constants of fine roots also varied with the method of calculating *k* (Table 3-6). For the same species, the *k* of fine roots based on regression was smaller than that calculated from single harvest time approach (Table 3-6). The decomposition rate-constants of red alder, Douglas-fir, western hemlock, and ponderosa pine were 0.316, 0.219, 0.222, 0.247/year (regression approach) in comparison to 0.398, 0.278, 0.266, and 0.303/year (single harvest time approach), respectively.

3.4.2.3.2 Small roots

Similar to fine roots, no significant site effects were observed in the decomposition rate-constants of small roots (Figure 3-5 and Figure 3-8). However, species influenced the *k* of small roots significantly. Comparing the average *k* of small roots at three sites, ponderosa pine was the fastest decomposing species among 8 small root species, with a decomposition rate-constant of 0.23/year (Table 3-6). The slowest *k* for small roots was western hemlock which had a value of 0.06/year. The second slowest species was Douglas-fir with a *k* of 0.073/year. Of the 8 species examined, the order of increasing average *k* was western hemlock < Douglas-fir < incense-cedar < Pacific rhododendron < red alder < antelope-brush < golden chinkapin < ponderosa pine (Table 3-6). With the exception of ponderosa pine, the roots of deciduous species decomposed faster than coniferous species.

Table 3-6. Decomposition rate-constants (k) of woody roots at Oregon sites.

Root type	Species	k (/year)	se	R^2	N	Half-life(yr)
Fine roots	red alder	0.316[a]	0.095	0.74*	6[b]	2.2
		0.398	0.066		3[c]	1.7
	ponderosa pine	0.247[a]	0.035	0.89**	8[b]	2.8
		0.303	0.080		3[c]	2.3
	Douglas-fir	0.219[a]	0.038	0.85**	8[b]	3.2
		0.278	0.082		3[c]	2.5
	western hemlock	0.222[a]	0.038	0.85**	8[b]	3.1
		0.266	0.052		3[c]	2.6
	Oregon ash	0.503	0.025		3[c]	1.4
	California red-fir	0.423	0.055		3[c]	1.6
	white fir	0.373	0.050		3[c]	1.9
	bigleaf maple	0.360	0.010		3[c]	1.9
	red maple	0.353	0.023		3[c]	2.0
	western redcedar	0.320	0.030		3[c]	2.2
	noble fir	0.317	0.025		3[c]	2.2
	lodgepole pine	0.313	0.021		3[c]	2.2
	Engelmann spruce	0.243	0.015		3[c]	2.9
	nut pine	0.237	0.052		3[c]	2.9
	incense-cedar	0.227	0.023		3[c]	3.1
Small roots	ponderosa pine	0.230	0.036		3[c]	3.0
	golden chinkapin	0.190	0.092		3[c]	3.6
	antelope-brush	0.160	0.070		3[c]	4.3
	red alder	0.153	0.070		3[c]	4.5
	Pacific rhododendron	0.137	0.038		3[c]	5.1
	incense-cedar	0.107	0.006		3[c]	6.5
	Douglas-fir	0.073	0.006		3[c]	9.5
	western hemlock	0.060	0.000		3[c]	11.6
Medium roots	red alder	0.084	0.042		3[c]	8.3
	lodgepole pine	0.060	0.008		3[c]	11.6
	Douglas-fir	0.060	0.008		3[c]	11.6
	ponderosa pine	0.042	0.012		3[c]	16.5
	western hemlock	0.031	0.006		3[c]	22.4
Large roots	Douglas-fir	0.065	0.018		3[c]	10.7
	lodgepole pine	0.060	0.017		3[c]	11.6
	ponderosa pine	0.028	0.021		3[c]	24.8
Jumbo roots	ponderosa pine	0.027	0.015		3[c]	25.7
	lodgepole pine	0.018	0.011		3[c]	38.5

a The k was based on the regression of single-exponential model. * $0.05 > P > 0.01$; ** $P < 0.01$. Other k was calculated from equation $k=Ln(d_f)/t$ where d_f is remaining mass percent at time t year.
b Each data point is the mean of 12 samples at three sites. c Each data point is the mean of 4 reps.

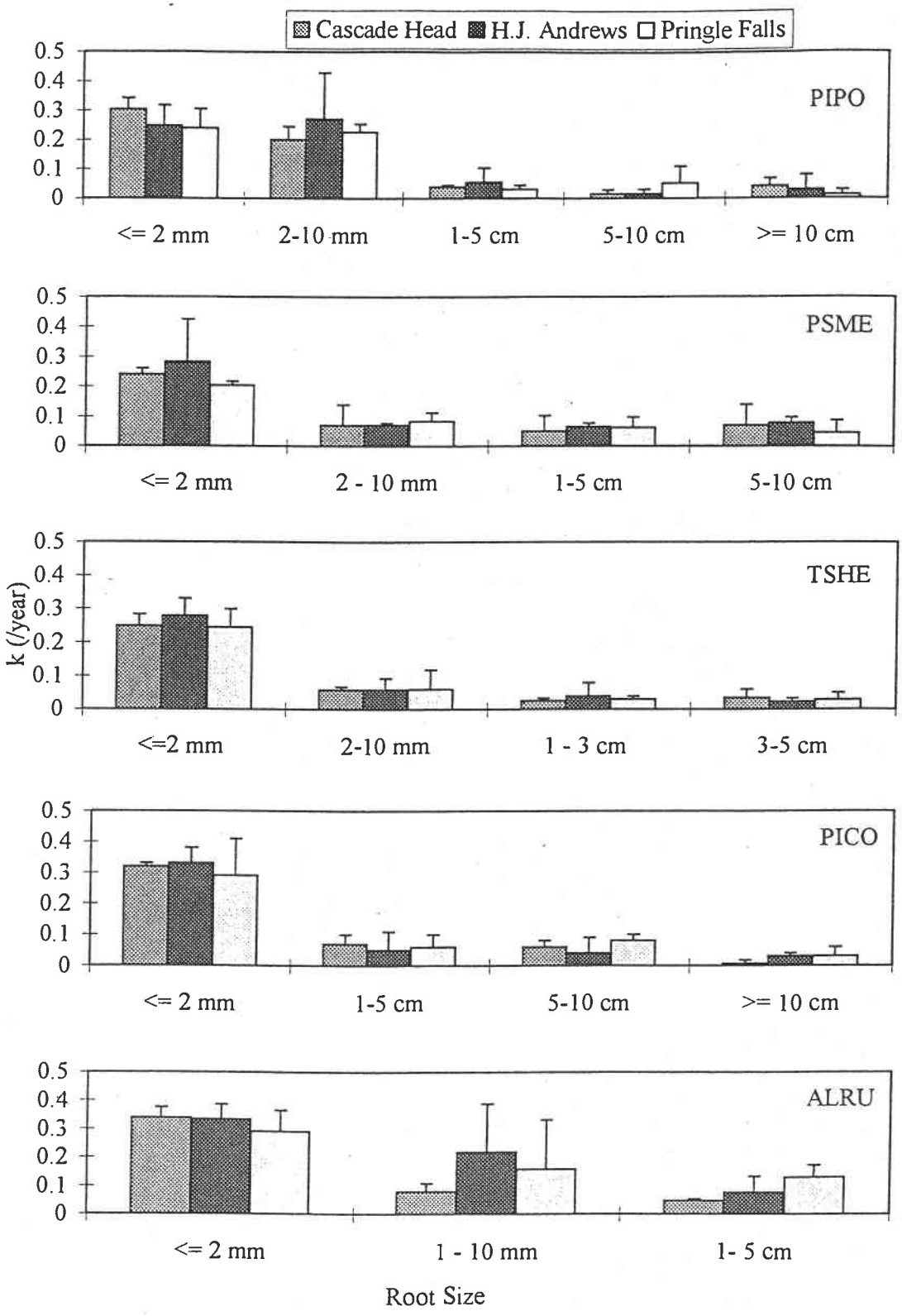

Figure 3-8. Root size and site effects on decomposition rate-constant of woody roots.

3.4.2.3.3 Medium, large, and jumbo roots

For medium roots, site did not appear to influence *k* significantly (Figure 3-8). The average decomposition rate-constant order for the 5 species examined was western hemlock < ponderosa pine < Douglas-fir < lodgepole pine < red alder, although their differences were not significant.

Site did not show significant effects on decomposition of large or jumbo roots (Figure 3-8). For large roots, Douglas-fir was the fastest decomposing species, lodgepole pine intermediate, and ponderosa pine the slowest, although their differences were not significant (Table 3-6). The decomposition rate-constants of ponderosa pine and lodgepole pine jumbo roots were very small, with 0.027 and 0.018/year, respectively (Table 3-6).

3.4.3 Controls of woody root decomposition

3.4.3.1 Initial substrate quality

Initial substrate quality indices varied with species and root size. For the same species, size differences were observed in initial root nitrogen and carbon concentration (Table 3-7). In general, nitrogen concentration of roots decreased with root size. Fine roots had the highest nitrogen concentration among all root sizes in part because these fine roots were from nurseries. The average fine root nitrogen concentration of 15 species was 1.42, ranging from 0.88 to 2.19%, while the average of small, medium, large, and jumbo roots was 0.38, 0.3, 0.23, 0.23%, respectively. Initial carbon concentrations of fine roots averaged 46.1%, relatively lower than that of other size roots which ranged from 48.8 to 54.4%. However, no obvious differences of initialcarbon among the other four root sizes were observed. In general, smaller roots had lower C:N ratios than larger roots mostly due to their high nitrogen concentration. The average C:N ratio of fine roots was 34.8 while the C:N ratio of jumbo roots averaged 232. Water soluble extractives decreased with root size classes with the values of fine, small, medium, large, and jumbo roots being 23.4, 13.7, 10.4, 6.2, and 6.2%, respectively. Similarly, water soluble sugar concentration generally decreased

Table 3-7. Chemical characteristics of fresh woody roots for five size classes*.

Species	Size	% N	% C	C:N	% WS extractives	% NPE	% WS sugar	%WS phenols	%AS Cellulose
ABCO	Fine	1.6	45.1	28.8	21.3	6.0	3.0	3.5	50.0
ABMA	Fine	1.6	45.9	29.0	27.4	7.2	6.0	2.9	43.8
ABPR	Fine	1.7	44.7	26.1	23.2	7.8	5.0	2.9	47.0
ACMA	Fine	1.5	45.8	29.6	20.0	5.2	4.2	2.1	52.5
ACRU	Fine	2.2	46.3	21.1	24.0	4.1	5.8	2.9	46.4
ALRU	Fine	1.8	45.1	24.8	31.7	7.3	6.8	7.5	45.9
CADE	Fine	1.0	48.0	46.6	16.5	15.2	3.5	4.2	42.8
FRLA	Fine	1.2	46.0	37.4	28.7	5.8	7.5	2.2	49.6
PICO	Fine	1.7	46.2	27.8	25.0	3.8	5.5	2.0	44.9
PIEN	Fine	1.2	46.7	37.7	22.0	7.8	6.4	3.0	43.6
PIMO	Fine	0.9	46.3	52.9	16.9	16.1	4.3	2.1	41.3
PIPO	Fine	1.0	47.3	49.3	21.2	11.7	4.9	2.3	43.8
PSME	Fine	1.3	47.0	35.2	21.9	6.3	5.3	5.3	42.2
THPL	Fine	1.6	46.3	28.5	22.6	11.8	3.6	4.0	45.1
TSHE	Fine	0.9	45.2	48.1	28.0	7.5	6.6	6.2	42.9
	mean (se)	1.42(0.38)	46.1(0.9)	34.8(10.1)	23.4(4.3)	8.2(3.8)	5.2(1.3)	3.5(1.6)	45.5(3.2)
ALRU	Small	0.7	50.7	75.7	8.9	5.5	1.9	2.5	50.6
CADE	Small	0.3	49.9	146.6	9.3	4.6	1.5	2.2	55.2
PIPO	Small	0.3	50.1	158.4	13.1	17.4	2.8	2.1	47.4
PSME	Small	0.3	52.7	151.6	22.3	12.1	6.4	11.1	35.7
PUTR	Small	0.4	48.8	130.5	13.3	8.8	2.5	2.4	49.8
RHMA	Small	0.4	50.4	136.2	16.8	4.2	5.5	5.5	51.7
TSHE	Small	0.2	51.0	206.7	12.2	2.3	3.7	5.6	51.7
	mean(se)	0.38(0.13)	50.5(1.2)	143.7(39)	13.7 (4.6)	7.8(5.3)	3.5(1.8)	4.5(3.3)	48.9(6.3)
ALRU	Medium	0.4	49.5	110.2	7.8	1.6	1.8	2.4	60.8
PICO	Medium	0.2	51.8	241.4	8.7	13.5	2.6	1.2	47.6
PIPO	Medium	0.3	51.1	149.0	7.7	6.0	2.1	1.9	58.8
PSME	Medium	0.3	51.6	190.1	10.2	5.7	2.2	4.3	49.8
PUTR	Medium	0.3	49.8	166.0	12.4	3.9	3.0	2.7	52.1
RHMA	Medium	0.3	49.4	173.8	16.7	5.5	4.5	4.3	55.2
TSHE	Medium	0.3	50.8	201.9	9.4	2.7	1.4	4.2	56.6
	mean (se)	0.3(0.08)	50.5(1)	176(41.5)	10.4 (3.2)	5.5(3.9)	2.5(1)	3(1.3)	54.4(4.8)
PICO	Large	0.3	51.6	183.4	5.7	7.7	1.3	0.9	50.0
PIPO	Large	0.1	54.4	362.7	5.3	16.6	1.2	0.8	50.4
PSME	Large	0.3	50.9	187.0	7.6	1.9	1.4	2.1	58.3
	mean (se)	0.23(0.07)	52.3(1.9)	244(103)	6.2 (1.2)	8.7(7.4)	1.3(0.1)	1.3(0.8)	52.9(4.7)
PICO	Jumbo	0.3	52.5	204.5	6.4	10.9	1.1	0.9	48.2
PIPO	Jumbo	0.2	51.2	260.3	6.1	3.0	1.3	1.6	56.1
	mean (se)	0.23(0.04)	51.9(0.9)	232(39)	6.2 (0.3)	7.0(5.6)	1.2(0.2)	1.2(0.5)	52.2(5.6)

Table 3-7. Continued.

Species	Size	%AIS lignin	%(lignin+ phenols)	Lignin:N ratio	Cellulose : N ratio	LCI ratio	LigCellu : N ratio	phenols : N ratio	LigPhen: N ratio
ABCO	Fine	22.7	26.2	14.5	31.9	0.3	46	2.3	16.7
ABMA	Fine	21.6	24.5	13.6	27.7	0.3	41	1.8	15.4
ABPR	Fine	22.0	24.9	12.9	27.5	0.3	40	1.7	14.6
ACMA	Fine	22.4	24.5	14.4	33.9	0.3	48	1.3	15.8
ACRU	Fine	25.5	28.4	11.6	21.2	0.4	33	1.3	12.9
ALRU	Fine	15.1	22.6	8.3	25.2	0.2	34	4.1	12.4
CADE	Fine	25.5	29.7	24.7	41.5	0.4	66	4.1	28.8
FRLA	Fine	15.9	18.1	12.9	40.3	0.2	53	1.8	14.7
PICO	Fine	26.2	28.2	15.8	27.1	0.4	43	1.2	17.0
PIEN	Fine	26.5	29.5	21.4	35.2	0.4	57	2.4	23.8
PIMO	Fine	25.6	27.8	29.3	47.2	0.4	76	2.4	31.7
PIPO	Fine	23.3	25.7	24.3	45.7	0.3	70	2.4	26.8
PSME	Fine	29.6	34.8	22.1	31.6	0.4	54	3.9	26.1
THPL	Fine	20.5	24.6	12.7	27.8	0.3	40	2.5	15.1
TSHE	Fine	21.6	27.8	22.9	45.6	0.3	69	6.6	29.6
	mean (se)	22.9(3.9)	26.5(3.8)	17(6)	34(8)	0.3(0.1)	51(14)	2.7(1.5)	20.1(6.8)
ALRU	Small	35.0	37.5	52.3	75.5	0.4	128	3.8	56.0
CADE	Small	30.9	33.1	90.9	162.3	0.4	253	6.3	97.3
PIPO	Small	22.2	24.3	70.0	149.9	0.3	220	6.7	76.7
PSME	Small	29.9	41.1	86.1	102.6	0.5	189	32.0	118.1
PUTR	Small	28.1	30.5	75.1	133.2	0.4	208	6.4	81.5
RHMA	Small	27.3	32.8	73.9	139.8	0.3	214	14.8	88.7
TSHE	Small	33.7	39.3	136.7	209.6	0.4	346	22.7	159.3
	mean (se)	29.6(4.3)	34.1(5.8)	84(27)	139(43)	0.4(0.1)	223(67)	13.2(10.6)	97(34)
ALRU	Medium	29.8	32.2	66.4	135.4	0.3	202	5.2	71.6
PICO	Medium	30.1	31.4	140.5	222.1	0.4	363	5.8	146.3
PIPO	Medium	27.5	29.5	80.3	171.4	0.3	252	5.6	85.9
PSME	Medium	34.3	38.6	126.4	183.8	0.4	310	15.7	142.1
PUTR	Medium	31.7	34.3	105.5	173.6	0.4	279	8.9	114.5
RHMA	Medium	22.6	26.9	79.5	194.2	0.3	274	15.1	94.6
TSHE	Medium	31.3	35.6	124.6	224.9	0.4	350	16.8	141.5
	mean (se)	29.6(3.7)	32.6(3.9)	103(28)	187(31)	0.4(0.0)	290(56)	10.5(5.2)	114(30)
PICO	Large	36.5	28.5	184.8	336.0	0.4	521	5.0	189.8
PIPO	Large	27.7	37.4	129.9	177.6	0.4	307	3.1	133.0
PSME	Large	32.3	34.4	118.5	214.2	0.4	333	7.8	126.3
		32.2(4.4)	33.4(4.6)	144(35)	243(83)	0.4(0.0)	387(117)	5.3(2.3)	150(35)
PICO	Jumbo	34.4	35.3	134.0	187.9	0.4	322	3.3	137.4
PIPO	Jumbo	34.8	36.4	177.0	285.2	0.4	462	8.0	184.9
		34.6(0.3)	35.8(0.8)	156(30)	237(69)	0.4(0.0)	392(99)	5.6(3.3)	161(34)

* WS extratives, water soluble extratives; NPE, nonpolar extratables(fats,oils, and waxes); WS sugar, water soluble carbonhydrate; WS phenols, water soluble phenols; AS cellulose, acid soluble cellulose and hemicellulose; AIS lignin, acid insoluble carbonhydrate and refers to lignin here. LCI ratio = lignin :(cellulose + lignin) where lignin and cellulose refer to AIS lignin and AS cellulose; LignCell refer to the summation of AIS lignin and AS cellulose in the LigCellu: N ratio; LigPhen refers to the summation of AIS lignin and water soluble phenols in LigPhen: N ratio.

with root size, averaging from 5.2% of fine roots to 1.2% of jumbo roots. Water soluble phenols concentrations, also appeared to decrease with root size. Cellulose and lignin increased with size, ranging from 45.5% and 22.9%, respectively in fine roots to 52.2% and 34.6%, respectively in jumbo roots.

There were also some interspecific differences in initial nitrogen and carbon concentration of roots within a root size class (Table 3-7). In general, roots of deciduous trees had higher nitrogen concentration than those of coniferous trees. For example, the nitrogen concentration fine roots of four deciduous trees averaged 1.7%, ranging from 1.2 to 2.2%, whereas nitrogen averaged 1.3% in coniferous fine roots, ranging from 0.9 to 1.7%. Similarly, the lignin concentration of coniferous species was relatively higher than the concentration of deciduous species, although the small roots of red alder were an exception.

Decomposition rate-constants (k) of fine roots were influenced significantly by their initial substrate quality, correlating significantly to 9 of the 17 initial chemical quality indices in the 15 fine root species (Table 3-8). Of the indices examined, the summation of lignin and phenols (LP), LP:N ratio, lignin:nitrogen ratio, and lignin-cellulose index (LCI) showed the best correlation with decomposition rate-constants of fine roots. The determination coefficients of these indices ranged from 0.63 to 0.69. There was correlation among the 17 indices examined, however, we listed each to find the best predictor of fine root decomposition. The multiple regressions indicated that best model for predicting fine root decomposition of all species was:

$$k = 0.736 - 0.903 * \text{LCI} - 0.006 * (\text{lignin} + \text{phenols}):\text{N}$$

This model was highly significant ($P < 0.01$) with a determination coefficient (R^2) of 0.83.

Effects of initial substrate indices on k of fine roots varied with coniferous and deciduous roots (Table 3-9 and Figure 3-9). When the four deciduous species were excluded from the analysis, the best predictive model of k contained only the lignin:N ratio. In contrast, the decomposition of 4 deciduous fine roots was associated with the summation index of lignin and phenols, although this model was not significant ($P = 0.06$).

Table 3-8. Effects of initial substrate index on decomposition rate-constants (k) of fine roots*.

Initial substrate index	F	df	P	R^2
Carbon	4.36	1, 14	0.06	0.25
Nitrogen	4.56	1, 14	0.05	0.26
Carbon: Nitrogen ratio	2.89	1, 14	0.11	0.18
NPE	**5.79**	**1, 14**	**0.03**	**0.31**
WS extractives	**9.84**	**1, 14**	**0.01**	**0.43**
WS sugar	2.21	1, 14	0.16	0.15
WS phenols	0.07	1, 14	0.80	0.00
Phenols : N ratio	2.48	1, 14	0.17	0.14
AS cellulose	**11.66**	**1, 14**	**0.01**	**0.47**
AIS Lignin	**16.2**	**1, 14**	**0.00**	**0.55**
Lignin + phenols	**22.36**	**1, 14**	**0.00**	**0.63**
(Lignin + phenols) : N	**25.79**	**1, 14**	**0.00**	**0.66**
Lignin : N ratio	**26.17**	**1, 14**	**0.00**	**0.67**
Cellulose : N ratio	2.89	1, 14	0.11	0.18
(Lignin + cellulose): N	**8.21**	**1, 14**	**0.01**	**0.39**
LCI ratio	**29.02**	**1, 14**	**0.00**	**0.69**
Lignin: phenols	0.52	1, 14	0.48	0.04

* NPE, nonpolar extratables (fats, oils, and waxes);
WS extratives, water soluble extratives;
WS sugar, water soluble carbonhydrate;
WS phenols, water soluble phenols, expressed as % tannic acid equivalents.
AS cellulose, acid soluble cellulose and hemicellulose;
AIS lignin, acid insoluble part including lignin and other recalcitrant carbon, refer to lignin in our study.
LCI ratio = Lignin:(cellulose+lignin) where lignin and cellulose refer to AIS lignin and AS cellulose;
Lignin and cellulose in (Lignin+cellulose):N ratio refer to AIS lignin and AS cellulose;
Lignin and phenols in (Lignin + phenols) index refer to AIS lignin and water soluble phenols;
Statistically significant sources of variation in decay rate-constant ($P <= 0.05$) are boldfaced.

Table 3-9. Final predictive model of root decomposition rate-constants (k).

Root type / model	n	F	P	R^2
Fine roots k = 0.736 - 0.903* LCI - 0.006 * LPN	15	28.38	0.0001	0.83
Coniferous fine roots k = 0.477 - 0.01*(lignin: nitrogen)	11	24.83	0.0008	0.73
Deciduous fine roots k = 0.755 - 0.015 * (lignin + polyphenol)	4	14.26	0.060	0.88
Small roots k = 0.224 - 0.006* (polyphenol : N)	7	13.68	0.014	0.73
Medium + large + jumbo roots k = 0.011 - 0.139 * nitrogen	10	4.75	0.061	0.37

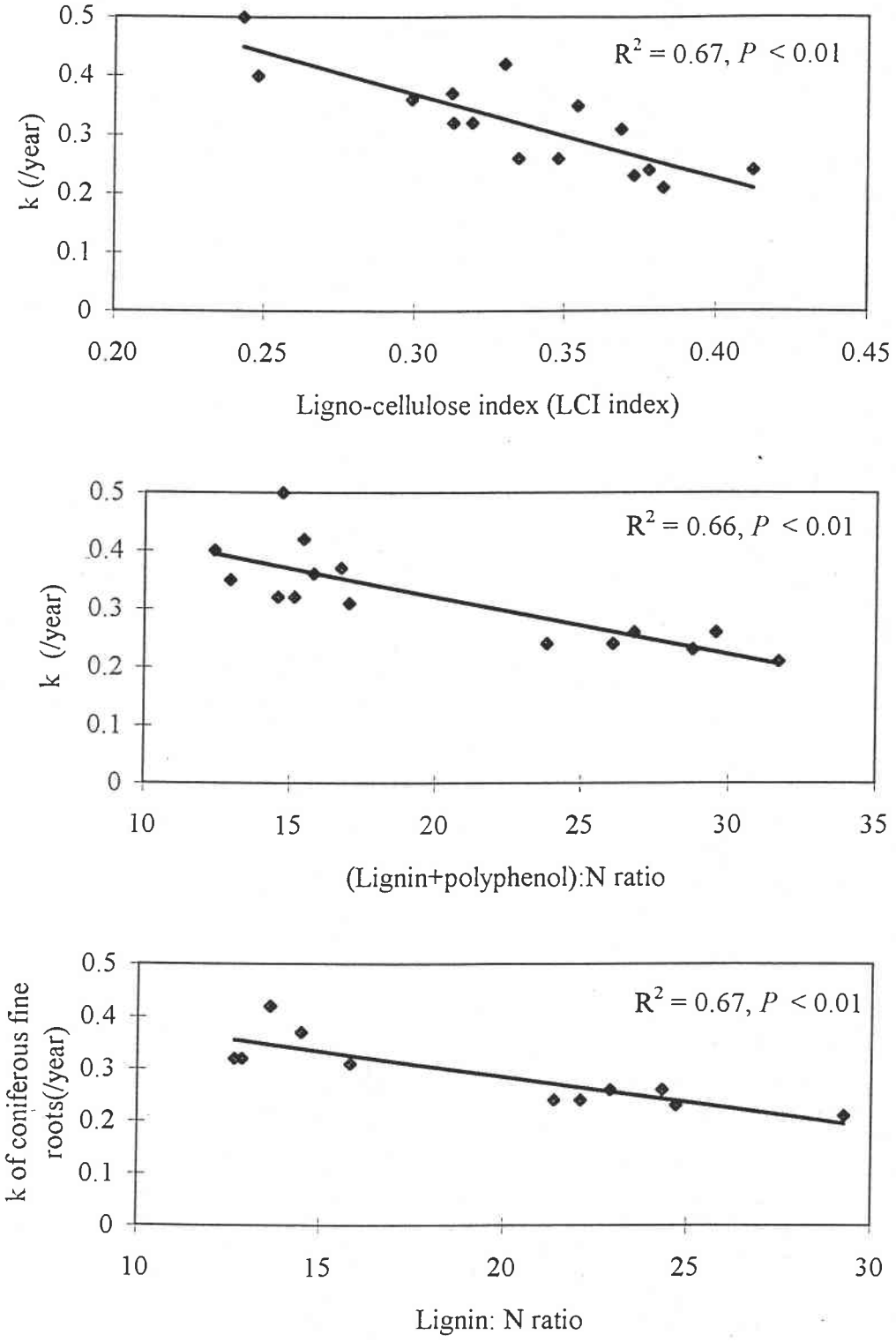

Figure 3-9. Decomposition rate-constants (k) of fine roots versus initial substrate quality indices.

For small roots, water soluble phenols, phenols:N ratio, lignin-phenols, and lignin:phenols ratio were the only indices of the 17 examined that correlated significantly with decomposition rate-constants (Table 3-10). The determination coefficient (R^2) ranged from 0.62 to 0.73; phenols:N ratio possessing the highest R^2 (0.73). This was further substantiated by the final multiple-regression model (Table 3-9) in which the phenols:N ratio was the only index present.

In contrast, none of 17 substrate indices was significantly correlated with k of woody roots larger than 1 cm in diameter. Nitrogen was the only index showing a close to significant ($P = 0.061$) correlation with k of larger woody roots (Table 3-9).

3.4.3.2 Root sizes and bark proportions

Most species exhibited a clear increase in half-life as root diameter increased (Figure 3-10). This pattern was most dramatic when the root diameter changed from fine roots (< 2 mm) to small roots (2-10 mm). For example, the half-life of western hemlock increased from 2.6 years at fine roots to 11.6 years at a 10-mm diameter. This pattern occurred in all 4 backbone species.

Bark proportions of woody roots varied with species, but declined with increasing root size (Figure 3-11a). Douglas-fir had the highest bark proportions among the five species examined, regardless of root classes. In comparisons with medium roots, red alder had the smallest bark proportions, about 10% of root volume. However, the correlation between bark proportion (Figure 3-11a) and k of woody roots (Figure 3-11b) was not significant ($P = 0.51$).

3.4.3.3 Effects of soil nitrogen availability

The ion exchange resin bags indicated there were significant differences in soil nitrogen availability among the three sites, as estimated by soil ammonium availability ($P = 0.007$) (Table 3-11). Soil ammonium availability of CAH was 98.99 μg/g air-dry resin, the highest among three sites. HJA and PRF had very similar soil ammonium availability values and showed significantly lower nitrogen availability than CAH. In contrast, there was no clear difference of soil nitrate availability index among three sites

Table 3-10. Effects of initial substrate index on *k* of small roots *.

Initial substrate index	F	df	*P*	R^2
Carbon	3.59	1, 6	0.12	0.42
Nitrogen	0.25	1, 6	0.64	0.00
Carbon: Nitrogen ratio	0.07	1, 6	0.80	0.01
NPE	0.51	1, 6	0.51	0.09
WS extractives	2.45	1, 6	0.18	0.33
WS sugar	4.77	1, 6	0.08	0.49
WS phenols	**8.71**	**1, 6**	**0.03**	**0.64**
Phenols : N ratio	**13.68**	**1, 6**	**0.01**	**0.73**
AS cellulose	1.4	1, 6	0.29	0.22
AIS Lignin	1.19	1, 6	0.33	0.19
Lignin + phenols	**7.94**	**1, 6**	**0.04**	**0.61**
(Lignin + phenols) : N	5.22	1, 6	0.07	0.51
Lignin : N ratio	2.31	1, 6	0.19	0.32
Cellulose : N ratio	0.07	1, 6	0.80	0.01
(Lignin + cellulose): N	0.49	1, 6	0.52	0.09
LCI ratio	4.55	1, 6	0.09	0.48
Lignin: phenols	**8.3**	**1, 6**	**0.04**	**0.62**

* NPE, nonpolar extratables (fats, oils, and waxes);
WS extratives, water soluble extratives;
WS sugar, water soluble carbonhydrate;
WS phenols, water soluble phenols, expressed as % tannic acid equivalents.
AS cellulose, acid soluble cellulose and hemicellulose;
AIS lignin, acid insoluble part including lignin and other recalcitrant carbon, refer to lignin in our study.
LCI ratio = Lignin:(cellulose+lignin) where lignin and cellulose refer to AIS lignin and AS cellulose;
Lignin and cellulose in (Lignin+cellulose):N ratio refer to AIS lignin and AS cellulose;
Lignin and phenols in (Lignin + phenols) index refer to AIS lignin and water soluble phenols;
Statistically significant sources of variation in decay rate-constant ($P <= 0.05$) are boldfaced.

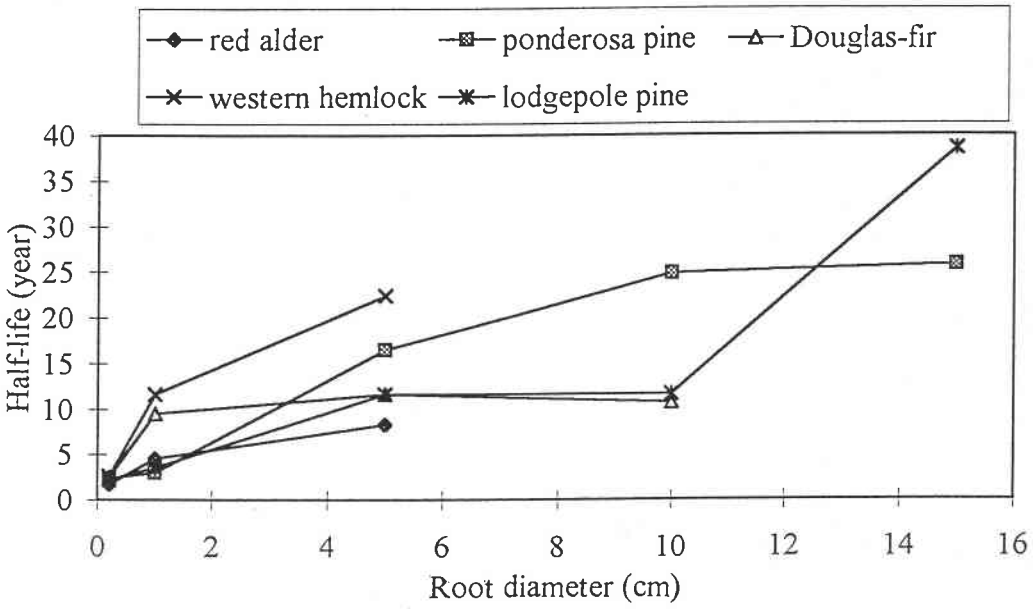

Figure 3-10. Effects of root size on the half-life of decomposing woody roots.

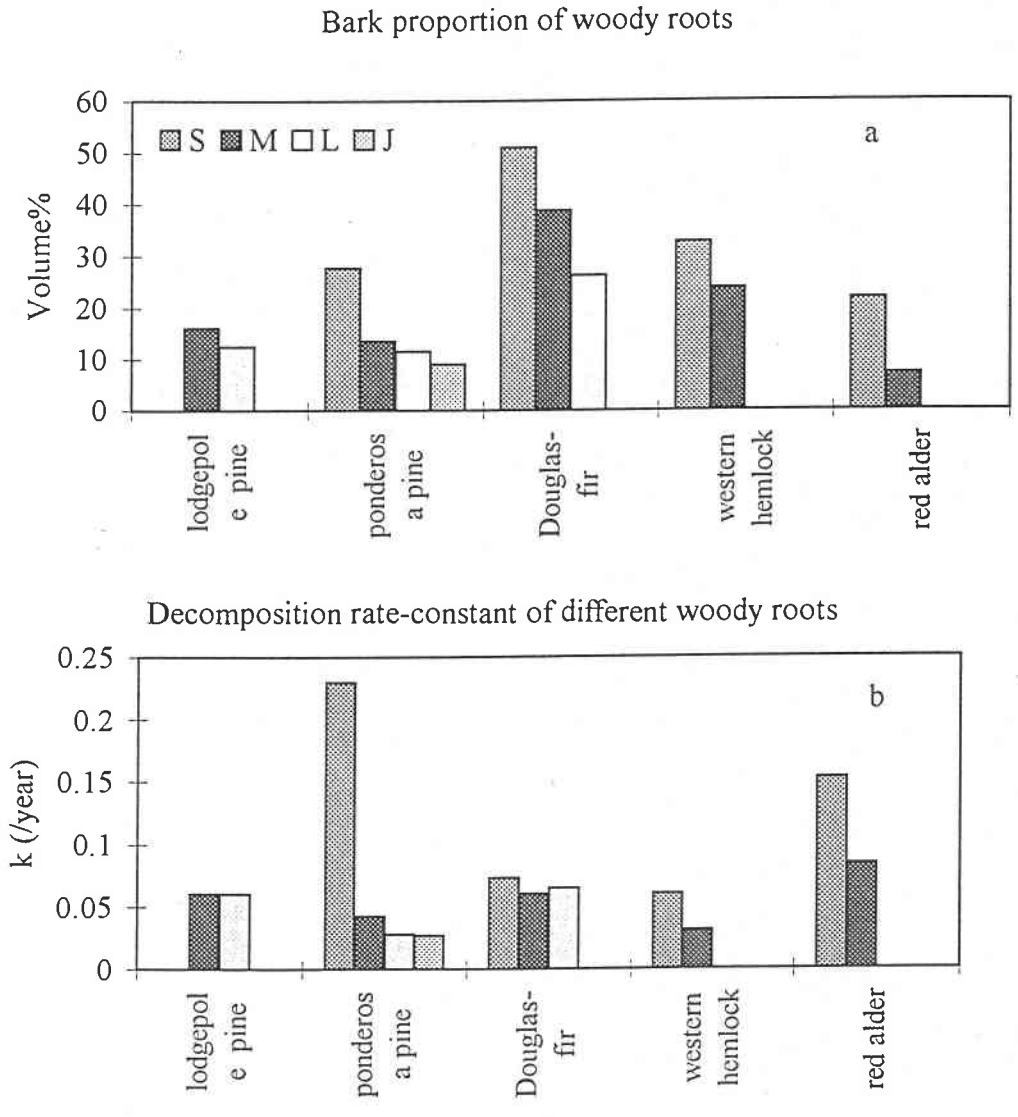

Figure 3-11. The relations of bark proportion and decomposition rate-constants of woody roots.

S:small roots (2-10 mm); M:medium roots (10-50 mm);
L:large roots (50-100 mm); J:jumbo roots (100 mm).

Table 3-11. Soil nitrogen availability index among three sites*.

Site	Nitrogen Availability Index (ug/g air-dry resin)		
	$NH4^+$	$NO3^-$	$NH4^+ + NO3^-$
Cascade Head	98.99[a] (59.08)	8.06[a] (9.74)	107.05[a] (59.14)
H.J. Andrews	19.07[b] (8.12)	2.75[a] (0.65)	21.82[b] (7.8)
Pringle Falls	19.10[b] (17.53)	9.97[a] (6.25)	29.07[b] (21.53)

*: the number in parenthesis is standard error. Values in a column followed by a different letter are significantly different ($P < 0.05$).

(P = 0.30), which ranged from 2.75 to 9.97 μg/g air-dry resin. The soil nitrogen availability index combining NH_4^+ + NO_3^- showed significant differences among three sites (P = 0.01), which was consistent with the pattern of soil NH_4^+ availability among three sites.

The decomposition rate-constant of woody roots was not correlated with soil ammonium availability (P = 0.39, R^2 = 0.23), despite the differences observed between sites. As we observed in Table 3-3 and Table 3-6, decomposition rate-constants of woody roots were not significantly different among three sites, although the fastest decomposing woody roots occurred more often at HJA or CAH than PRF. This suggests that soil nitrogen availability had little direct impact on the decomposition rate-constant of woody roots.

3.4.4 Carbon and nitrogen dynamics of roots

3.4.4.1 Carbon loss

The pattern of carbon loss during woody root decomposition was very similar to that of mass loss (Figure 3-12). The similarity of these two curves was due to the consistent carbon concentration of roots during decomposition, which was around 50% of dry weight as reported by other studies of wood detritus (Chen and Xu 1992, Harmon and Chen 1991, Harmon et al. 1986). In order of increasing average carbon loss of fine roots at three sites after 2 years of decomposition the species were: incense-cedar (39.0%) < nut pine (45.5%) < Engelmann spruce (43.8%) < Douglas-fir (44.1%) < western hemlock (46.0%) < ponderosa pine (46.5%) < lodgepole pine (47.7%) < western redcedar (48.0%) < noble fir (49.6%) < bigleaf maple (52.6%) < red maple (53.0%) < white fir (53.2%) < red alder (54.1%) < California red-fir (57.0%) < Oregon ash (65%), very close to the order of the decomposition rate-constants of fine roots.

The carbon loss pattern of small, medium, large, and jumbo roots was very similar to their mass loss. At the end of first year of decomposition, small roots of western hemlock, antelope-brush, Douglas-fir, and ponderosa pine averaged 5.5%,

9.8%, 11.7%, and 22.5% losses of initial carbon contents, respectively. The large roots of ponderosa pine, Douglas-fir, and lodgepole pine lost 7.4%, 8.1%, and 8.2% during the same period. The jumbo roots of ponderosa pine released only 4.6% carbon in first year of decomposition. However, medium roots released less carbon in the first year decomposition. In order of increasing average carbon loss the species were western hemlock (1.7%) < ponderosa pine (2.3%) < red alder (3.9%)< lodgepole pine (8.5%) < Douglas-fir (11.6%).

3.4.4.2 Nitrogen dynamics

3.4.4.2.1 Fine roots

The nitrogen content of fine roots exhibited a quick decrease in first 3 months, then showed either a consistent declining trend over time or a short phase of nitrogen accumulation thereafter. For all species, however, more nitrogen was released than accumulated in first 2 years of fine root decomposition (Figure 3-12). This pattern was observed at all three sites (Figure 3-12a, b, c). Red alder and Douglas-fir experienced a consistent nitrogen release during the first 2 years of decomposition at all three sites. However, ponderosa pine and western hemlock started to accumulate some nitrogen after the initial rapid release of nitrogen.

In general, nitrogen was released from fine roots more slowly than mass or carbon (Figure 3-12). Exceptions occurred in red maple and lodgepole pine from which more nitrogen was released than mass in 2 year of decomposition. Species differed markedly in the total net N released during decomposition, with fast decomposing species generally releasing more nitrogen than slow decomposing species. For example, Oregon ash fine roots released almost half of their initial nitrogen during the first 2 years of decomposition, whereas incense-cedar only lost 26% of its initial nitrogen content during the same period. In increasing order of nitrogen release from 15 fine roots in 2 years of decomposition, the species were incense-cedar (26.1.0%) < ponderosa pine (29.6%) < western hemlock (32.1%) < nut pine (35.3%) < Douglas-fir (37.2%) < Engelmann spruce (38.7%) < Oregon ash (44.8%) < bigleaf maple (45.3%)

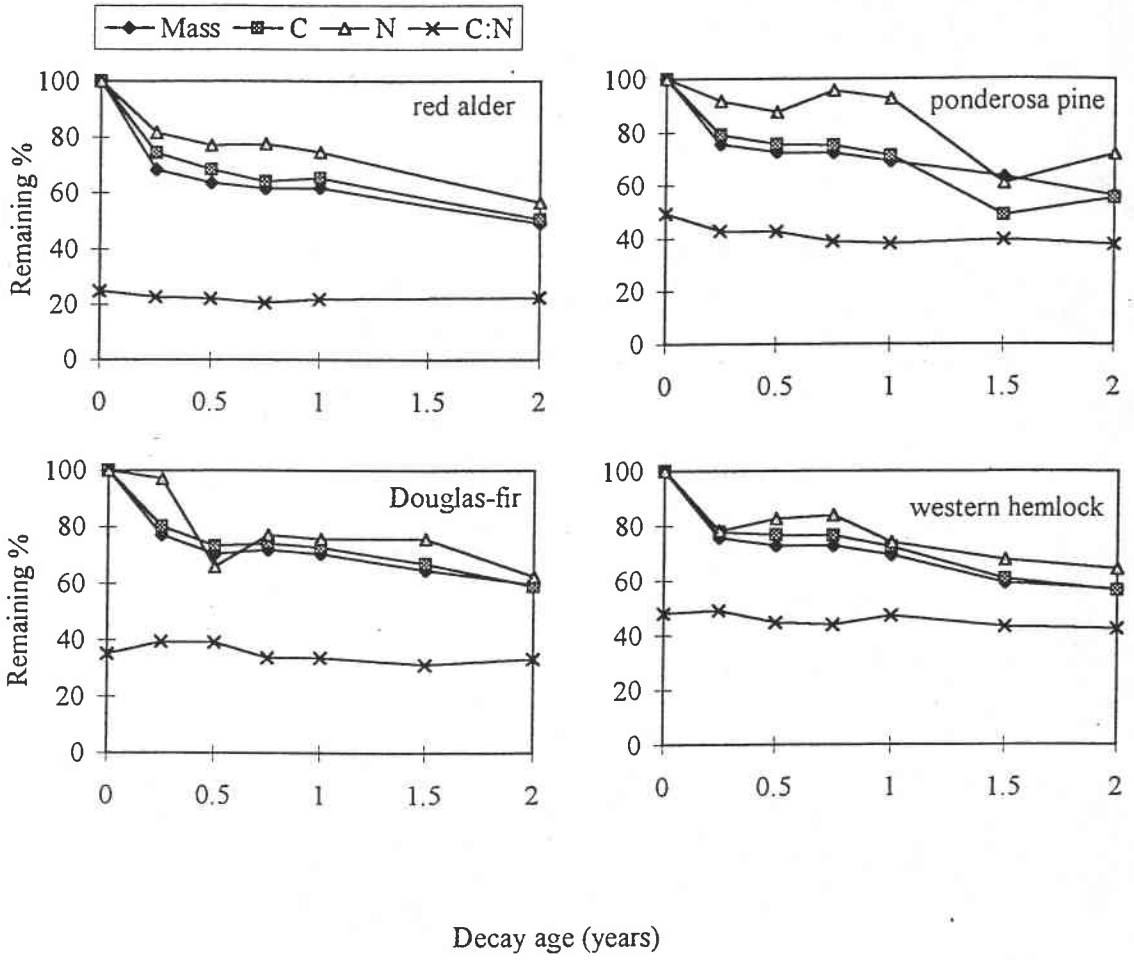

Figure 3-12a. Mass, C, and N dynamics in fine root decomposition at the CAH site.

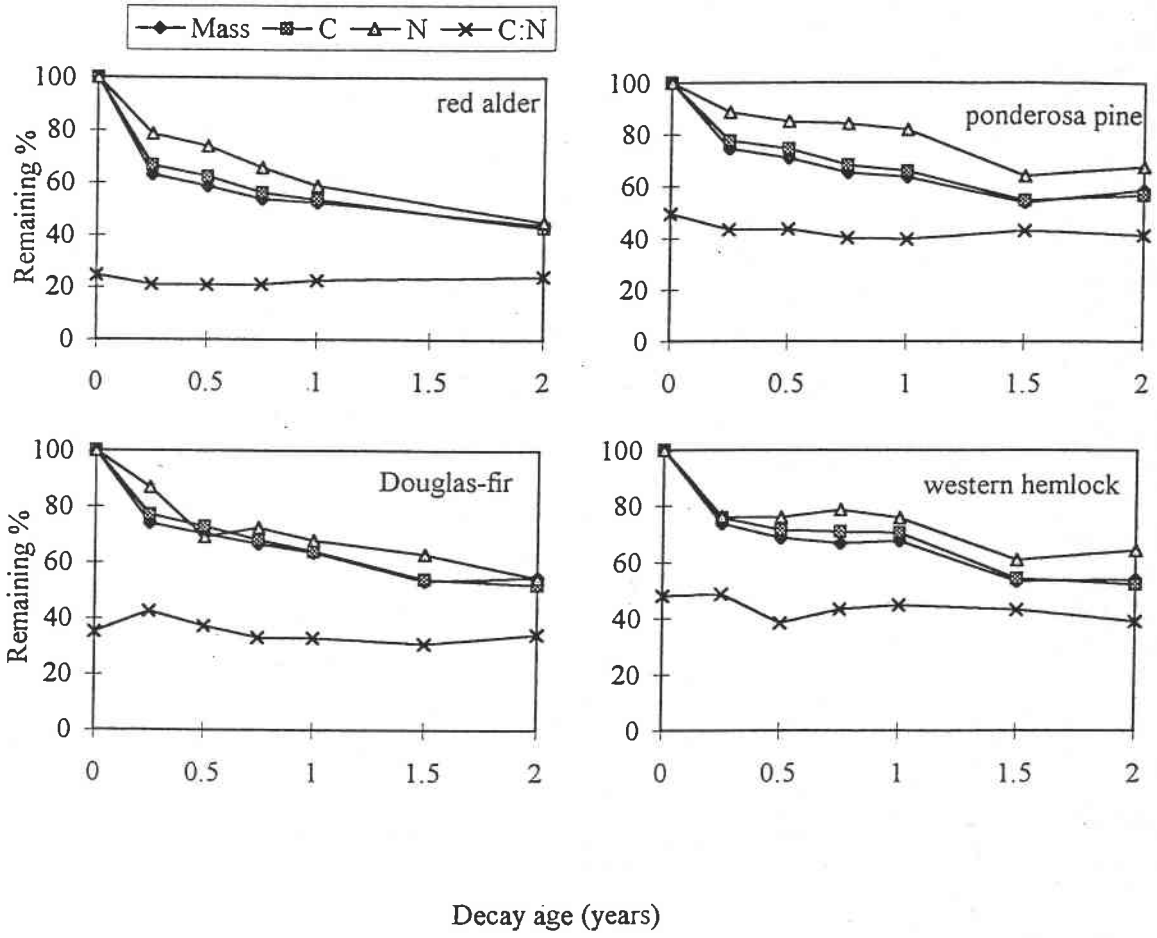

Figure 3-12b. Mass, C, and N dynamics in fine root decomposition at the HJA site.

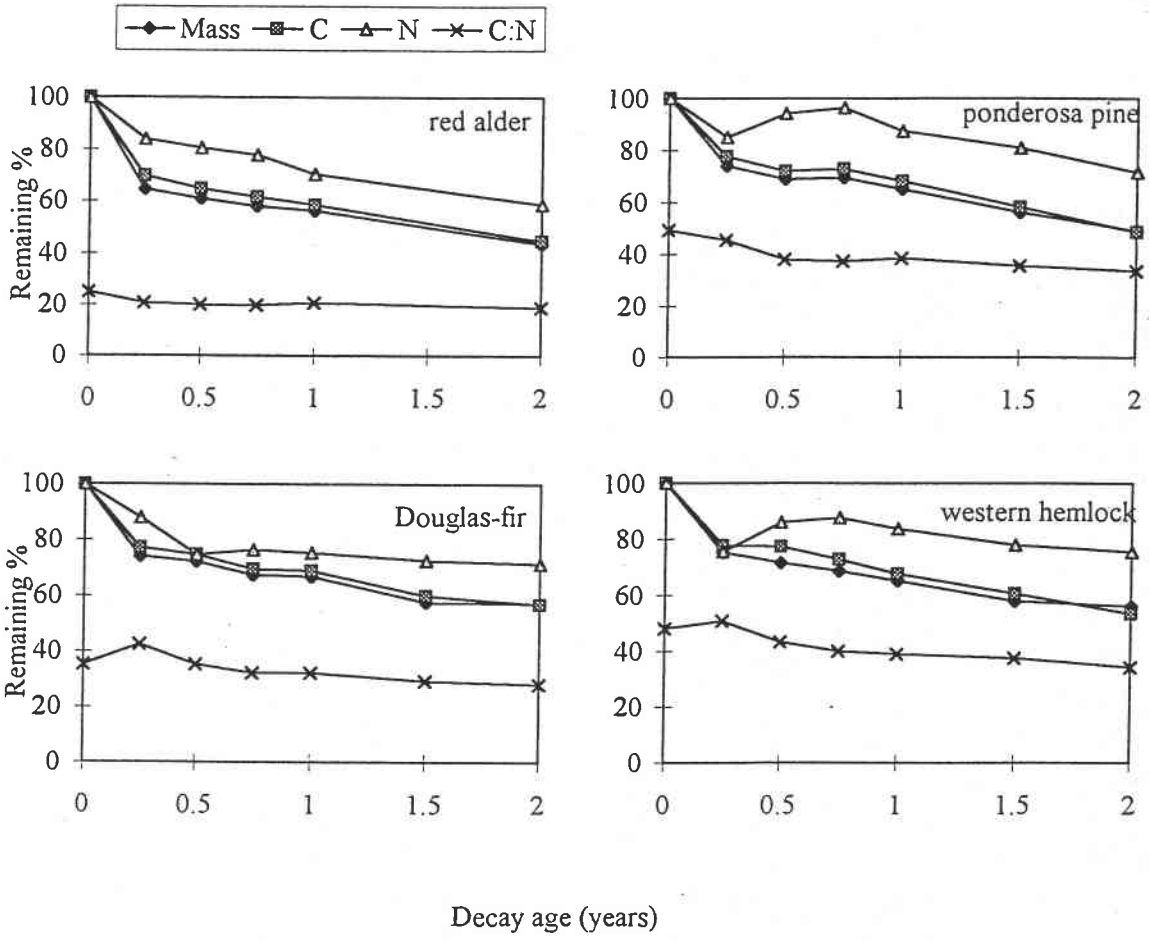

Figure 3-12c. Mass, C, and N dynamics in fine root decomposition at the PRF site.

< noble fir (46.2%) < red alder (46.6%) < western redcedar (48.8%) < white fir (49.7%) < lodgepole pine (50.1%) < California red-fir (51.1%) < red maple (63.1%). This order was not exact the same with the mass loss order of fine roots, suggesting the nitrogen loss pattern was not always correlated with mass loss (Figure 3-12).

The C:N ratio of decomposing fine roots did not change greatly during the 2 years of decomposition, although a declining trend existed generally (Figure 3-12). For example, the C: N ratio of fresh fine roots of red alder, ponderosa pine, Douglas-fir, and western hemlock were 24.8, 49.3, 35.2, and 48.1. This narrowed to 18.9, 33.6, 28.0, and 34.2, respectively by the end of 2 years of decomposition at CAH.

3.4.4.2.2 Small, medium, and other size roots

Dynamic patterns of nitrogen content of woody roots varied with species, and root size, but not with sites (Figure 3-13). For small roots, ponderosa pine and Douglas-fir released nitrogen during the first year of decomposition among three sites, while western hemlock and antelope-brush accumulated nitrogen in the same period (Figure 3-13a). For medium roots, ponderosa pine, Douglas-fir, and western hemlock released nitrogen in the first year of decomposition, regardless of sites (Figure 3-13b). In contrast, medium roots of red alder accumulated almost 50% nitrogen in first year at all three sites. In between, lodgepole pine released about 10% nitrogen at HJA and PRF, but accumulated 20% nitrogen at CAH. For large roots, Douglas-fir and lodgepole pine released a small fraction of nitrogen (< 5%) in the first year decomposition at the three sites whereas ponderosa pine accumulated nitrogen except for CAH site (Figure 3-13c). Of the jumbo roots, ponderosa pine, released about 10-20% of original nitrogen in first year of decomposition across three sites (Figure 3-13c).

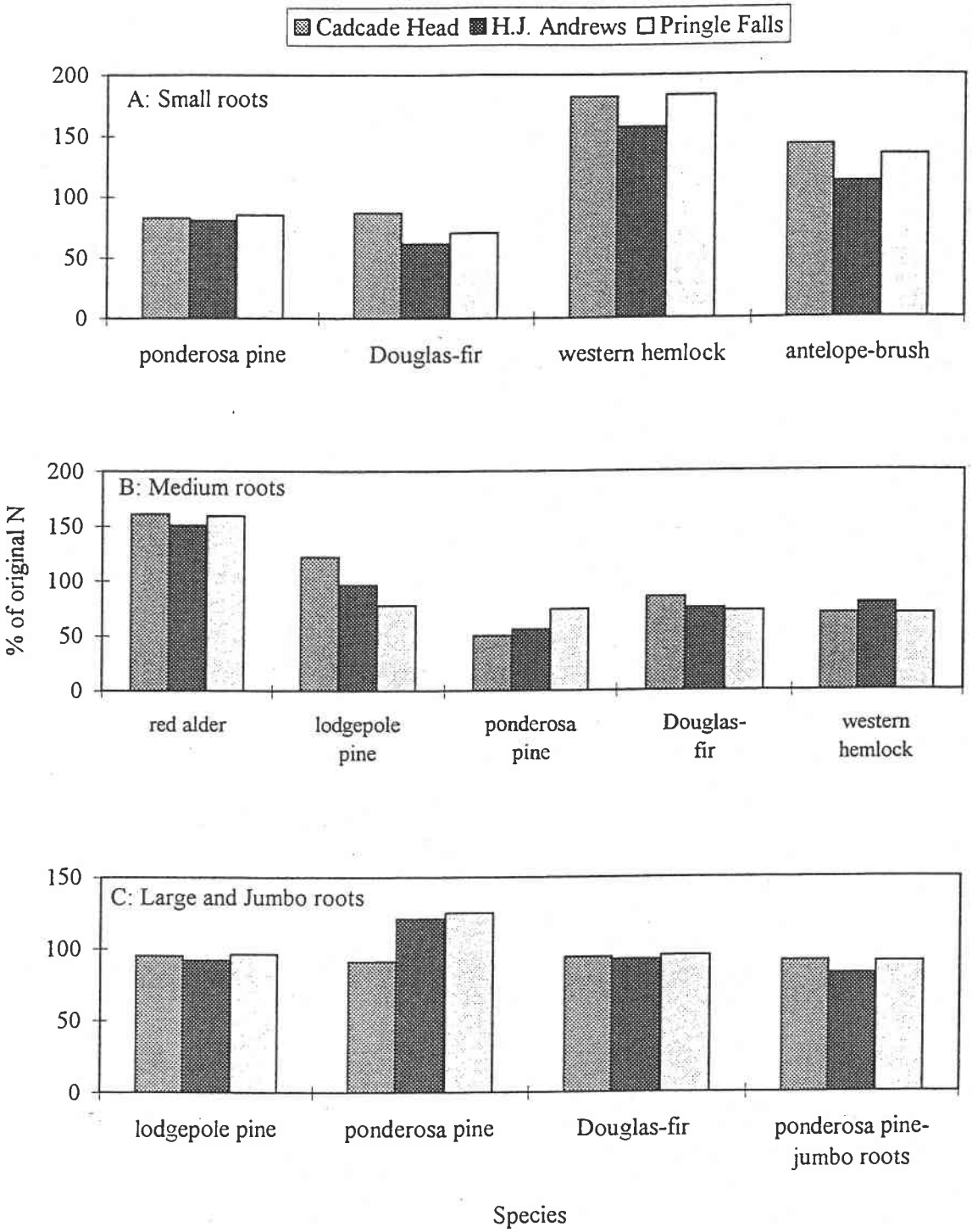

Figure 3-13. N content of woody roots after 1 year decomposition at three sites.

3.5 DISCUSSION

3.5.1 Controls of woody root decomposition

3.5.1.1 Biotic factors - initial substrate quality

Litter decomposition is profoundly influenced by litter substrate quality as well as climatic environment and decomposer community (Heal et al., 1997; Swift et al., 1979). The initial rapid mass loss observed may be due to leaching and/or microbial respiration of labile compounds. As fine roots have much higher concentrations of labile compounds than larger woody roots (Table 3-7), the former should exhibit a large initial mass loss whereas the latter should not. In this study, the fine roots of the 4 "backbone" species lost 25-30% of their initial mass in the first 3 months of decomposition, accounting for more than 50% of the accumulated mass loss during the first 2 years of decomposition, regardless of site (Figure 3-4). A similar pattern was reported in other root decomposition studies (Fahey et al., 1988; Harmon, unpublished data; Lohmus and Ivask, 1995; McClaugherty et al., 1984;). McClaugherty et al. (1984) found the fine roots (< 3 mm) of red pine and hardwoods in temperate forests of the northeast USA lost 10 to 20% of their initial mass during the first year of decomposition, then the rates slowed down significantly. In a northern hardwood forest, Fahey et al. (1988) observed that the decomposition of fine roots (< 0.6 mm) was rapid in the first summer of incubation (May-July), averaging 22%. Similarly, in Norway spruce forests, Lohmus and Ivask (1995) indicated that Norway spruce fine roots (< 1mm) lost 19.4% of initial mass during the first 3 months (July-September). McClaugherty et al. (1984) further indicated that no systematic differences were observed among mass losses in studies begun in February, November, and July. At HJA, the LIDET (Long-Term Intersite Decomposition Experiment Team) study indicated that one-third of the initial mass loss of three fine roots (*Drypetes glauca*, *Pinus elliotii*, and *Andropogon gerardii*) occurred in the first year (Harmon, unpublished data). Gower observed similar initial fine root rapid mass loss in boreal forests (personal communication, 1998). The similarity in the patterns of fine root

mass loss, regardless of season, site location or forest type, suggests that this initial rapid mass loss is due more to physical processes such as leaching, than to microbial processes which are more temperature sensitive.

Melillo et al. (1989) suggested lignin-cellulose index (LCI) as an indicator of plant material's susceptibility to microbial attack because as the LCI increases, plant litter becomes increasingly resistant. Our study suggests that the same phenomenon occurs in fine root decomposition. This index is based on the fact that lignin, an important component of cell walls, is the most recalcitrant component in plant tissue decomposition (Berg, 1984; Bloomfield et al., 1993; Fogel and Cromack, 1979; Melillo et al., 1982). In general, LCI is lower in deciduous fine roots than coniferous ones, providing a partial explanation for why the decomposition rate-constant is higher in deciduous than in coniferous fine roots. The analysis of coniferous fine roots further confirmed that the lignin:N index was the best predictor of k among all the indices in our study with an inverse relationship with the decomposition rate-constant k. Our results are therefore in agreement with other root decomposition studies (Berg, 1984; Melillo et al., 1982; McClaugherty et al., 1984). Given the few studies on root decomposition, the effects of climatic variables (e.g., mean annual temperature, precipitation, and actual evapotranspiration) on the relationship between k and lignin:N ratio of fine roots are not clear. After examining the decomposition of aboveground litters from a wide range of species, Harmon et al. (1990) concluded that decomposition in temperate forests was not strongly influenced by climatic variables. This is consistent with the lack of site effects in our study. In our study, phenols: nitrogen ratio was inversely correlated to k of small roots. This is probably due to the recalcitrant nature of phenols (Bloomfield et al., 1993, Palm and Sanchez, 1991). Some phenols have the ability to form complexes with tissue proteins, making them less vulnerable to attack by decay organisms and can bind decomposer enzymes, thereby reducing or eliminating their activity (Bloomfield et al., 1993). In one study of the decomposition rate-constant of leguminous leaf litter in tropical agroecosystems, tissues with high nitrogen and phenol concentrations were recalcitrant to decomposition (Palm and Sanchez, 1991).

Initial substrate indices were poor predictors of k values in larger size class roots (diameter > 1 cm) for the first 2 years of decomposition. None of 17 substrate indices including LCI index, LP:N ratio, lignin:N, and phenols:N ratio was significantly correlated to k. This may be due to the short decomposition period used in our study relative to the time required to decompose larger roots. When modeling root decomposition, a structural component-oriented approach may provide a better solution to predicting the long-term woody root decomposition than initial substrate indices (see Chapter 2) because woody roots of various species have qualitative and quantitative differences in root structural components, especially in term of bark proportions. However, the correlation between bark proportions and k of woody roots was not significant ($P = 0.51$). Studies with longer incubation times may be needed to demonstrate differences in decomposition rates of different large root tissues.

Root size controlled root decomposition. Most species exhibited a clear increase in half-life as root diameter increased (Figure 3-10). Our results were consistent with Fahey et al. (1988) who indicated the decomposition of small roots (0.6 to 10 mm diameter) decreased with increasing root size in a northern hardwood ecosystem. The cause of this pattern is attributed to the poorer substrate quality of large woody roots which are characterized by low water soluble extractives, high lignin content, and low N (Table 3-7). Moreover the low surface area:volume ratio may require a longer period for decomposers to colonize large roots (Harmon et al., 1986).

3.5.1.2 Abiotic factors - different decomposition environments

The global gradient of increasing soil organic matter with increasing latitude strongly indicates the controls of temperature and moisture over the decomposition (Schlesinger, 1996). However, both factors appeared to have been of minor importance controlling fine root mass loss during the first two years of decomposition. No significant differences in root or dowel mass loss were observed among the CAH, HJA, and PRF sites even thought there were large climatic differences between these sites. Temperature and moisture may still have played a role in root decomposition

given the fact that woody roots at HJA and CAH generally decomposed faster than the roots at PRF (Table 3-5, Figure 3-7, Figure 3-8).

Why were there no large differences between these sites? First, soils play a buffering role in reducing the extremes of soil temperature and moisture. Yearly fluctuations in soil temperature at 20-cm depth were about 14 °C, 12 °C, and 5 °C at PRF, HJA, and CAH, respectively (Figure 3-14b), considerably less than those in air (Figure 3-14a). The annual precipitation at PRF was only 15% of CAH and 22% of HJA. Despite this, decomposing roots were not as dry as we had expected at PRF, staying above 100% moisture content all year round (Figure 3-15). This indicates that, within the range of precipitation at sites observed, the soil can keep the decomposing roots wet enough to maintain the microbial processes throughout the year. This suggests that the differences in the belowground environments among the three sites is not as large as those aboveground. The comparison of aboveground and belowground dowel decomposition at these three sites supports this hypothesis (Figure 3-3).

Second, the dominant environmental limiting factors appear to have varied with site. Low soil temperature at PRF and high root moisture at CAH appear to have limited the microbial processes and in turn slow down root decomposition. In contrast, the combination of soil temperature and moisture regimes at HJA is the best among the three sites resulting in the fastest root decomposition. Soil temperature at PRF could reach as low as 1^0 C in winter and early spring (Figure 3-14b) and this cold period lasted several months which would have retarded the activity of decomposers (Chen and Harmon, unpublished data). The negligible mass loss of fine roots in winter and early spring at PRF was consistent with this hypothesis (Figure 3-16). Although the lowest soil temperature for HJA was around 2^0 C in December, it persisted for a much shorter period than at PRF. Therefore the low temperature at HJA probably had little effect on root decomposition. CAH showed the most favorable thermal conditions among the three sites, ranging from 7 to 14 °C year round. However, the moisture content of dead roots at CAH usually was between 300 to 450%, and occasionally it could reach as high as 500%. This high moisture content may have reduced oxygen

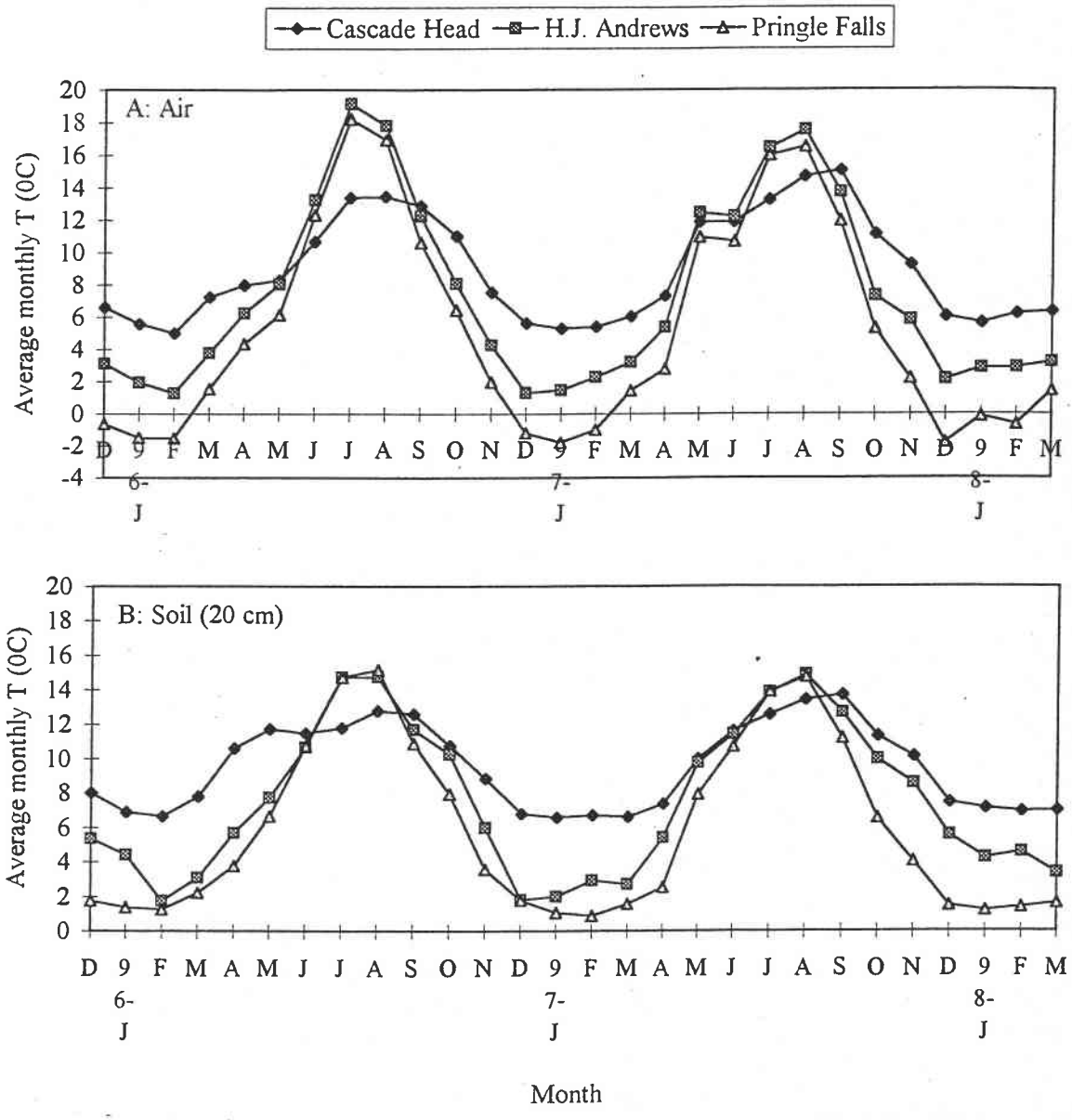

Figure 3-14. Seasonal patterns of air and soil temperature of three sites*.

*: each point was the mean temperature of 3-4 plots.

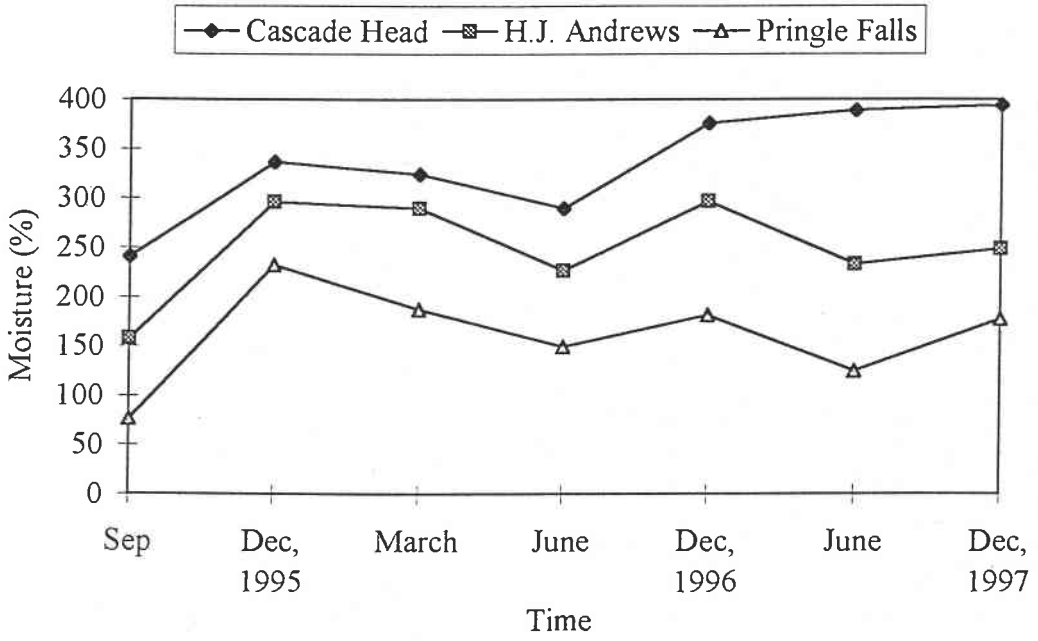

Figure 3-15. Moisture dynamics of fine roots at three sites.

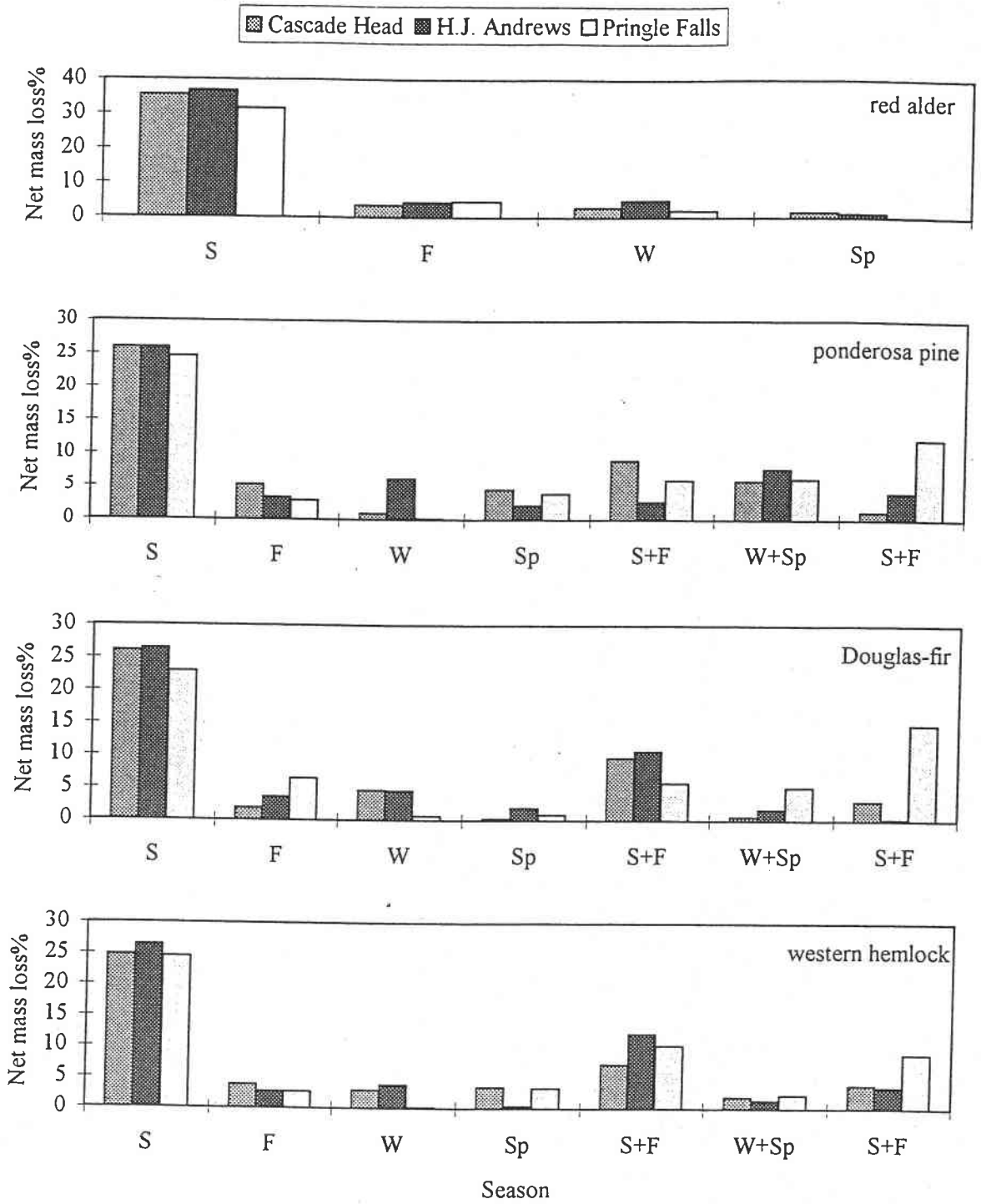

Figure 3-16. Seasonal patterns of fine root decomposition at three sites*.

* S, F, W, and Sp are summer (June-Aug.), fall (Sept.-Nov.), winter (Dec.-Feb.),and spring (March-May).

diffusion in the belowground system, and may have resulted in anaerobic conditions which would hinder the decomposition of roots.

3.5.2 Decomposition rate-constants (k) of fine roots and litterbag techniques

The differences in k of fine roots are not only controlled by biotic and abiotic factors such as species, climate but also influenced by methods used to calculate k. For the same species, the k of fine roots based on regression was smaller than that calculated from single harvest time approach (Table 3-6). For the same species, the k values of both approaches should be similar if fine roots decomposed in a negative exponential manner. In fact, fine roots did not decompose linearly with time, showing a rapid mass loss in early stages, then slowing down (Figure 3-4). This pattern would have caused the single harvest estimate to be higher than the regression method based on the data of multiple harvests.

The decomposition rate-constants of fine roots in our study are comparable to the results of other fine root decomposition studies conducted in the Pacific Northwest (Table 3-6 and Table 3-12). The k of 15 fine roots ranged from 0.219 to 0.423/year, compared with k values of 0.163/year (Fogel and Hunt, 1979), 0.245/year (Sollins et al., 1981), and 0.124-0.237/year (Harmon, unpublished data) of fine roots in Oregon and Washington. Although Vogt et al. (1983) reported that the decomposition rate-constant of *Abies amabilis* was as high as 0.708/year, this probably was due to the very small fine roots (< 1 mm in diameter) examined in their study. Comparing the same species, Douglas-fir, we observed that k was 0.219/year (using regressions approach) or 0.278/year (using one-harvest) in present study, whereas Sollins et al. (1981) reported the k was 0.245/year (using one-harvest). The relatively high k of fine roots in the present study probably is due to their relatively high N and low lignin concentration (Table 3-7 and Table 3-12).

Litterbag techniques may underestimate root decomposition rate-constants for several reasons. Large soil organisms are excluded by the bags and consumption would be minimized and fungal colonization may be delayed. Rhizosphere organisms that could play a role in decomposition may have been killed or separated from the

Table 3-12. Summary of decomposition rate-constants (k) of roots from literature.

Species	Diameter (mm)	k (/yr)	Half-life (year)	Method to get k	Period of decay (years)	Lignin (%)	N (%)	References
Pseudotsuga	2--3	0.245a*	2.82	One-harvest	0.52	ND	0.42	Sollins et al.
menziesii	3--5	0.240a*	2.89	One-harvest	1	ND	0.28	1981
Oregon								
Pseudotsuga	< 5	0.163a	4.33	Regression	2	ND	0.54	Fogel and Hunt
menziesii								1979
Oregon								
Drypetes	< 2	0.237a	2.92	Regression	5	16.13	0.76	Harmon,
glauca								unpublished
Pinus elliotii	< 2	0.124a	5.59	Regression	5	34.9	0.82	data
Andropogon	< 2	0.192a	3.61	Regression	5	10.54	0.63	
gerardii								
Oregon								
Abies amabilis	< 1	0.708b	0.98	Regression	2	33.2	0.86	Vogt et al.
Washington								1983
Pinus strobus	0.5--3	0.299a	2.32	Regression	4	25.3	0.93	McClaugherty
Wisconsin								et al. 1984
Hardwood	< 0.5	0.125a	5.54	Regression	4	21.9	1.32	McClaugherty
Massachusetts	0.5--3	0.271a	2.56	Regression	4	23.3	0.85	et al. 1984
Acer saccharum	0.5--3	0.178a	3.89	Regression	4	33.8	1.67	McClaugherty
Massachusetts								et al. 1984
Pinus resinosa	< 0.5	0.151a	4.59	Regression	4	21.8	1.2	McClaugherty
Massachusetts	0.5--3	0.207a	3.35	Regression	4	21.6	0.8	et al. 1984
Hardwood	0.6-1.0	0.171a*	4.05	One-harvest	1.9	28.6	1.09	Fahey et al.
	1.0-2.5	0.188a*	3.69	One-harvest	1.9	26.5	0.95	1988
Picea rubens	0.6-1.0	0.151a*	4.59	One-harvest	1.9	25.8	1.11	
New Hampshire	1.0-2.5	0.158a*	4.39	One-harvest	1.9	23.4	0.78	
Dacryodes	< 2	0.83a	0.83	Regression	1	28.7	3.9	Bloomfield
excelsa								et al. 1995
Prestoea	< 2	0.60a	1.16	Regression	1	26.8	2.5	
montana								
Puert Rico								

a: litterbag technique; b: trench plot technique.

*: the k was calculated based on the remaining mass data of roots provided by the paper.

ND: not determined.

roots during sample preparation, altering the normal decomposition process mediated by rhizosphere organisms including mycorrhizal fungi (Fahey and Arthur, 1994; McClaugherty et al., 1984). However, compared to trench plot techniques (Vogt et al., 1983), laboratory incubation method (Taylor and Parkinson, 1988), and other indirect measurement of fine roots decomposition (Aber et al., 1985), litterbag techniques are attractive in their simplicity, convenience, and reasonably reliable results. As long as their limitations are recognized, this method still has an important role to play in the decomposition study of organic matter, especially combined with more sensitive measures such as isotope labeling.

3.5.3 Nitrogen dynamics

Decomposing fine roots released nitrogen from the earliest decomposition stages across all three sites. A similar trend was observed in the decomposition of all small roots except western hemlock and antelope-brush after one year of decomposition (Figure 3-13a). The net result is that decomposing roots were net nitrogen sources during the first two years of decomposition. This is in agreement with several other root decomposition studies. Parker et al. (1984) found nitrogen was released in decomposing roots of a desert annual after one month of decomposition. Newman and Eason (1989) observed that the buried grass roots of *Lolium perenne* lost about half their nitrogen in three weeks, but only one-fifth of the dry weight. Seastedt et al. (1992) found dead grassland roots released N at the start of decomposition. Hobbie (1996) found several roots of shrub and trees from Alaska tundra lost N immediately following incubation in microcosms, although some N immobilization occurred in the later decomposition stages. In an agroecosystem study, Andren et al. (1990) reported net mineralization from four of five root litters examined. These studies showed that the pattern of nitrogen dynamics of dead roots were quite different from that of aboveground fine litter which generally accumulated nitrogen over extended periods (Aber et al., 1990; Berg and Ekbohm, 1983; Gosz et al., 1973; Melillo et al., 1982; Staaf and Berg, 1981). In contrast, roots tend to start to release nitrogen from the earliest stages of decomposition. Although initial fine root nitrogen

concentrations from seedlings grown in nurseries were 30 - 60% higher than fine roots collected in forests, the nitrogen release observed probably is not simply due to the fact we used nursery fine roots.

Decomposing woody roots can be an important nitrogen source after large-scale disturbances such as the harvest of aboveground biomass or forest fire. Taking into account the biomass of woody roots, initial nitrogen concentrations, and our decomposition data we can make preliminary estimates of the total amount of nitrogen released from woody roots after a catastrophic disturbance. After forest clear-cut or forest fire, an average of 200 Mg/ha of dead root biomass is created in old-growth Douglas-fir forests at Pacific Northwest (Vogt et al., 1986). We assumed these roots are composed by 10, 20, 50, and 120 Mg/ha fine, small, medium, large-jumbo roots, respectively and that among these roots, Douglas-fir and western hemlock comprised 60% and 40%, respectively. Using the data from our study, we estimated that as a result of a catastrophic disturbance in old-growth Douglas-fir forests, about 70 kg/ha nitrogen would be released annually from decomposing woody roots during the first two years. About one third of this would be released from fine roots. The amount of nitrogen released from dead roots is very large compared to other nitrogen inputs to old-growth Douglas-fir forests; e.g., annual N input as precipitation and dust is 2.0 kg/ha, 2.8 kg/ha is fixed by cyanophycophilous lichens in the canopy, and 3.3 kg/ha/year N is returned to the forest floor by microparticulate litterfall (Sollins et al., 1980). Following catastrophic disturbance dead woody roots can therefore not only release an impressive amount of N, but also may provide it at a time when the forest ecosystem has a high demand for this nutrient.

3.6 CONCLUSIONS

Species significantly influenced mass loss in both fine and small roots, whereas site had little influence during two years of decomposition study. In contrast, no significant species or site effects were found in medium, large, jumbo woody root decomposition. For fine roots, Oregon ash, the fastest among 15 species examined lost about 63% of initial mass after two years. In contrast, incense-cedar, the slowest, lost

only about 35% of its initial mass during the same period. The mass loss curves of Douglas-fir, western hemlock, and ponderosa pine were very similar, losing about 40% of their initial dry weight in 2 years. All fine roots had a period of rapid mass loss during the first 3 to 6 months, accounting for more than 50% of total mass loss in the first two years. For small roots, ponderosa pine showed the fastest decomposition, losing 36% of its initial dry weight during 2 years. In contrast, western hemlock and Douglas-fir of the same size were the most decomposition resistant species losing between 11% and 14% of their initial mass for the same period. The order of increasing average k of small roots was western hemlock (0.06/year) < Douglas-fir (0.073/year) < incense-cedar (0.107/year) < Pacific rhododendron(0.137/year) < red alder (0.153/year) < antelope-brush (0.16/year) < golden chinkapin (0.19/year) < ponderosa pine (0.23/year). For larger size class roots, roughly ≤ 10% of initial mass was lost in 2 years. The decomposition of woody roots decreased with increasing root size. Although the net results of root decomposition among three sites were similar, there appeared to be some consistent temperature and moisture effects on root decomposition. Soil nitrogen availability had no direct influences on woody root decomposition despite a 5 - fold difference among sites.

Initial substrate quality indices proved to be a good predictor of k for fine and small roots. For all fine roots, lignin-cellulose index (LCI) and lignin-phenols:N accounted for 83% of the variation of decomposition rate-constants. Furthermore, lignin:N ratio alone was the best predictor of k for coniferous fine roots. For small roots, phenols: N ratio was the best predictor of k, accounting for 73% of the variation.

Decomposing fine and small roots started to release nitrogen from the earliest stages of decomposition. Decomposing roots, especially fine roots, could be an important nitrogen source with about 70 Kg/ha/year of nitrogen released from dead wood roots after catastrophic disturbances (e.g., clear-cut, forest fire) in Douglas-fir old-growth forests. Given the timing and amount of nitrogen released from dead roots, this pool may be vital for forest regrowth and forest ecosystem restoration.

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CHAPTER 4

EFFECTS OF TEMPERATURE AND MOISTURE ON CARBON RESPIRED FROM DECOMPOSING WOODY ROOTS

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4.1 ABSTRACT

Controls of temperature and moisture on root decomposition have not been well studied despite their directly relevance to climate change impacts on root carbon flux. The main objective of this laboratory study was to examine the respiration response of Sitka spruce, Douglas-fir, western hemlock, ponderosa pine, and lodgepole pine decomposing roots (1-3 cm in diameter) to temperature and moisture change. Roots of Sitka spruce, Douglas-fir and western hemlock, ponderosa pine and lodgepole pine of different decay classes were collected from the Cascade Head, H.J. Andrews, and Pringle Falls sites, respectively. Dead root respiration increased with temperature and reached the maximum at 30- 40 °C, then decreased. ANCOVA indicated that the Q_{10} of root decomposition rate was influenced significantly ($P < 0.01$) by a incubation temperature range of 5-40 °C, but not by species, decay class or the direction of temperature change. At 5 - 10 °C, Q_{10} averaged 3.99 and then decreased to 1.37 at 30 to 40 °C. Over a range of 5-60 °C, Q_{10} could be predicted by a single-exponential model using temperature as the independent variable. ANOVA showed that the respiration rate of dead roots was significantly ($P < 0.01$) influenced by root moisture, species, and decay class as well as temperature. Dead root respiration increased with root moisture, reached the optimum range when moisture was between 100 and 275% and then decreased. Moreover, there were apparent interactions of root moisture and temperature on root respiration. Our study showed the direction of temperature and moisture change did not significantly influence root respiration, indicating hysteresis may not occur for the temperature and moisture ranges we examined. To better model global climate warming effects on root carbon flux, we suggest a temperature dependent Q_{10} function should be incorporated into current root dynamics models. The short-term laboratory incubation approach provided a good way to examine temperature and moisture controls on root decomposition, although we are cautious about long-term mass-loss extrapolations based on these short-term results.

4.2 INTRODUCTION

As researchers try to gain a better understanding of the possible impacts of global climate change on carbon and nutrient cycling in forest ecosystems and their feedback to climate, increasing attention is being focused on root dynamics belowground (Walker and Steffen, 1997). Root systems store large amounts of carbon and nutrients in forest ecosystems (Berg, 1984; Waid, 1974). More than 200 Mg/ha of root biomass has been estimated in old-growth coniferous forests of the Pacific Northwest of USA (Ehrenfeld et al., 1997; Nadelhoffer and Raich, 1992; Vogt et al., 1986, 1991). Experimental studies have indicated that photosynthetic rate is generally increased for plants grown in elevated CO_2 environment (Gunderson and Wullschleger, 1994; Strain, 1987) and this leads to additional carbon to be allocated to roots (Norby et al., 1987). Meanwhile, elevated atmospheric CO_2 changes may lead to a warmer, moister future climate (Houghton et al., 1996) which in turn would generally enhance root decomposition in forest ecosystems. The future carbon store and nutrient balance of forest ecosystems strongly depends on the degree that increased decomposition of roots is offset by increased production belowground.

Decomposition of roots, like other litters, is influenced by climatic environment as well as substrate quality and the decomposer community (Berg, 1984; Heal et al., 1997; McClaugherty et al., 1984, 1985; Swift et al., 1979). However, past studies on root decomposition have primarily focused on the influences of root substrate quality (Berg, 1984; Bloomfield et al., 1993; Camire et al., 1991; Fahey et al., 1988; McClaugherty et al., 1984), soil fauna, and soil type (Gijsman et al., 1997; Judas et al., 1995). Very few studies have dealt with the temperature and moisture controls on root decomposition (King et al., 1997). In contrast, the response to change of temperature, moisture, or both of aboveground litters is well known (Bartholomew and Norman, 1946; Boddy, 1983; Flanagan and Veum, 1974; Moore, 1986; O'Connell, 1990; Witkamp and Van der Drift, 1961). Experimental studies directly testing temperature and moisture controls on root decomposition, although few in number, are critical to developing a predictive understanding root decomposition (Berg, 1984; Camire et al., 1991; Waid, 1974).

Past studies indicate that litter respiration generally increases with increasing temperature and moisture in certain range (Bartholomew and Norman, 1946; Boddy, 1983; Flanagan and Veum, 1974; Moore, 1986; O'Connell, 1990; Taylor and Parkinson, 1988a, 1988b; Witkamp and Van der Drift, 1961). The temperature responses of root respiration is frequently expressed as a Q_{10} function which indicates the change in respiration rate for a 10 °C rise in temperature. The Q_{10} values of aboveground litters or soil organic matter appear to be higher in cold climate than in warm climatic regime (Kirschbaum, 1995; Schlesinger, 1977; Singh and Gutpka, 1977; Winckler et al., 1996). However, the effects of moisture, species, and decay class of dead roots on Q_{10} are simply unknown. Moreover, there are strong interactive effects of temperature and moisture on litter respiration (Boddy, 1983; Bunnell et al., 1977; Flanagan and Veum, 1974; Moore, 1986; O'Connell, 1990). Flanagan and Veum (1974) indicated that at lower moisture contents (< 50% of dry weight) temperature increases had little effect on respiration of tundra litters, but at higher moisture contents (100 - 225%), respiration was more responsive to temperature changes. Similarly, they noted that moisture changes had little effect on litter respiration at lower temperatures (< 5 °C), while at higher temperature (10 - 15 °C) respiration was more responsive to moisture changes. Too little or too much water inhibited or even stopped litter respiration due to matric limitation or oxygen diffusion limitation, respectively (Boddy, 1983; Bunnell et al., 1977; Flanagan and Veum, 1974). Does the respiration of decomposing roots respond similarly to changes of temperature and moisture to litters on the forest floor?

In addition to temperature and moisture responses, the presence of hysteresis effects of temperature and moisture on respiration of decomposing roots have not been tested, although they would be highly relevant. The earliest description of hysteresis appeared in physics and indicates that the relationship of a physical property (Y) and variable (X) is not unique, but dependent on whether X is increasing or decreasing. A good physical example is equilibrium soil water content which depends on whether the soil is drying or wetting (Brady and Weil, 1996). All current decomposition models assume hysteresis effects of temperature and moisture on litter decomposition are minimal (Jenkinson et al., 1991;

Potter et al., 1993; Raich and Potter, 1995; Raich et al., 1991), although this assumption has not been tested.

The objectives of this study were to: 1) examine the effects of temperature and moisture change on respiration of decomposing roots (1-3 cm in diameter) of Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), and lodgepole pine (*Pinus contorta*); 2) evaluate the possible interactions between temperature and moisture on root respiration; and 3) test for hysteresis effects of temperature and moisture on respiration of decomposing roots. Due to the complex covariance between temperature and moisture occurring in field sites, a laboratory incubation approach in which temperature and moisture regimes could be manipulated was used.

4.3 METHODS

4.3.1 Sites and sampling procedures

Decomposing woody roots of Sitka spruce, Douglas-fir, western hemlock, ponderosa pine, and lodgepole pine were collected from Sitka spruce, Douglas-fir, and ponderosa pine forests at Cascade Head Experimental Forests (CAH), H. J. Andrews Experimental Forests (HJA), and Pringle Falls Experimental Forests (PRF), respectively. CAH is located on the Pacific coast near 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 nitrogen. The dominant forest type is a mixture of western hemlock and Sitka spruce, although small stands dominated by Douglas-fir also occur (Franklin and Dyrness, 1973). HJA is located 80 km east of 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 20-60%. The forests are dominated by Douglas-fir and western hemlock at low elevation (1050-1550 m)

(Franklin and Dyrness, 1973). PRF is located in 57 km southwest 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 aerially 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).

Woody roots of Sitka spruce were taken from trees that were clear-cut 1, 12, and 20 years ago at CAH. Douglas-fir and western hemlocks were collected from trees cut 1, 15, and 20 years prior to sampling at HJA. Ponderosa pine and lodgepole pine were sampled from 3 stands which were clear-cut 2, 11, 23 years ago at PRF. These root samples were subjectively assigned to decay class I, II, and III, respectively, after referring to the decay class system of logs (Harmon et al., 1986). Class I was the least decayed and had the most extensive bark cover with a decay age of 0 to 3 years. Class II of roots, a decay age of 3 to 15 years, had most bark cover and root wood started to decompose. Class III was very decayed with some root wood left and bark had started to fall off. The decay age of class III was at least 20 years in this study. Root samples were collected in July of 1996 and May of.1997. At each root collection, two stumps of each species were selected at each stand. After excavating the soil surrounding the roots, 20 - 40 cm long root samples (1- 3 cm in diameter) were removed using a handsaw, labeled and put into a plastic bag as soon as possible to prevent water loss. Root samples were stored in a cooler during transportation and in a 1-2 °C degree walk-in cooler at Corvallis before laboratory incubation.

4.3.2 Incubation

Since our purpose was to understand the response of respiration of decomposing roots to temperature and moisture change, but not to measure the exact respiration rate of decomposing roots, a short term (4 hours) incubation of root samples was used. Roots collected from the three sites were cleared of surface soil first and then they were cut into 6 cm long segments. The wet weight of each segment was recorded and then each segment was tagged with a unique numbered aluminum tag

indicating the species, decay class, and replication number. Each root sample was placed in the bottom of a Mason jar (Ball Corp., Muncie, Indiana.) with a headspace of 500 ml.

Temperature effects. Root samples collected in July of 1996 were used to evaluate temperature effects on root respiration. Samples of known moisture content were incubated at different temperatures to examine temperature effects on root respiration. Thirty Mason jars with root samples were incubated at 0, 3, 5, 10, 15, 30, and 40 °C for 4 hours, respectively. For each type of root we had two replicates. Temperatures of individual roots were first increased from 0 to 40 °C and then decreased over the same series to test for possible hysteresis effects. After those incubations, the 30 samples were incubated at 50 and 60 °C to examine the high temperature effects on root respiration. Therefore, temperature range for laboratory incubation was from 0 to 60 °C. The incubation temperature gradient was created by a refrigerator from 0 to 40 °C. Beyond 40 °C, water baths of 50 and 60 °C were used. Preliminary studies indicated that the oxygen inside a Mason jar was sufficient for the incubated root segment to respire 4 hours at 30 °C at a rate that was not inhibited due to lack of oxygen (Chen and Harmon, unpublished data). Moisture content of root sample did not change very much after each 4 hour incubation (e.g. approximately 3.1 - 6.9% moisture was lost in each laboratory incubation.). Here we simply regarded the root moisture content unchanged during the incubations.

Moisture effects. Root samples collected in May of 1997 were used to examine the effects of moisture and possible interactions between moisture and temperature on root respiration. Root samples were wetted or air-dried to generate a moisture gradient ranging from water saturation to very dry. All incubated roots were started at highest moisture content (230~300%) by soaking in water 5 days and then dried to the lowest content (30~45%) and then rewetted to known moisture contents (60~120%, 120~180%, and 230~300%) until water saturation was reached. This design allowed us to test for hysteresis effects. At each moisture level, the root samples were incubated at 5, 15, and 30 °C to evaluate the interaction between temperature and moisture on respiration. For each type of root we had two replicates.

Carbon efflux. Increases of CO_2 concentrations in Mason jars were measured by gas chromatography (HP 5890 Series II) after each incubation. The Gas Chromatograph (GC) used a He carrier and a thermal conductivity detector (TCD). At least a 45 minutes period was used for the TCD to warm up and stabilize. A standard of 0.99% CO_2 gas was used and the GC was recalibrated if the standard CO_2 differed more than 0.05%. Preincubation of Mason jars was required at the incubation temperature for one hour before 0.5 ml of air inside a Mason jar was sampled using a syringe and measured by GC as the time zero value. Four hours later, another 0.5 ml air sample was injected and measured similarly. The net increase of CO_2 concentration during the 4 hours incubation at the temperature was used to calculate the respiration rate of the root. After all the required incubations were finished the root samples in Mason jars were oven-dried (65 °C) for a week and the oven-dry weight (ODW) recorded. The initial moisture content of the root sample was calculated using the initial wet weight and ODW. The respiration rate, k (μg carbon/g dry-root/hour), of decomposing root was calculated from the formula:

$$k = (\Delta CO2/100)*(1/ODW)*(1/IP)*(V)* 41.0339 * 12 \qquad (1)$$

where ΔCO2 is the net percent increase of CO_2 concentration during the incubation period, ODW oven-dry weight of root sample (g), IP incubation period (hour), V net volume of headspace (ml, 500 - volume of root sample), 41.0339 is the constant for converting CO_2 molar volume (ml) to micro mol at 25.9 °C laboratory temperature and 1 atmosphere pressure condition, and finally the whole formula is multiplied by 12 to convert micro mol of CO_2 to microgram of carbon.

The Q_{10} of respiration rate of decomposing roots in this study is calculated from the formula:

$$Q_{10} = (k_2/k_1)^{[10/(T2-T1)]} \qquad (2)$$

where k_2 and k_1 are the respiration rates of decomposing roots incubated at temperature T_2 and T_1 °C, respectively.

4.3.3 Data standardization and statistical analysis

Respiration rates of decomposing roots at different incubated temperatures and moisture were first standardized either for each species or for all species combined to reduce the confounding influences of decay classes and/or species in evaluating temperature and moisture effects on root respiration. In the analysis of temperature effects, we standardized the respiration rates of roots based on each species and all species combined. For each species, the relative respiration rate of roots was the ratio of respiration rate and the maximum respiration rate for the entire range of incubation temperatures. Similarly, the relative respiration rate of all species at a temperature was the ratio of mean respiration rate of all species at that temperature and the maximum mean respiration rate of the five species over the entire range of incubation temperatures. In the analysis of moisture effects, similar data standardization was conducted for each species based on three different incubation temperatures. Consequently, relative respiration rate of roots always was smaller than or equal to one.

Analysis of Covariance (ANCOVA) was used to test the effects of temperature range, species, decay class, and direction of temperature change on the Q_{10} of respiration rate of incubated roots. Root moisture was treated as a covariance in this analysis. Two-way Analysis of Variance (ANOVA) was used to test how moisture, temperature, species, and decay class control root respiration. Differences between means were detected using Fisher's Protected Least Significant Difference (LSD). All statistical tests were performed by procedure GLM of SAS Institute, Inc. (1985). Statistical tests were judged significant if $0.05 > P > 0.01$ and highly significant if $P \leq 0.01$.

4.4 RESULTS

4.4.1 Temperature effect

The five different species responded to temperature change similarly with the relative respiration rate of roots increasing with incubation temperature, reaching a

maximum at 40 °C, and then decreasing above that temperature (Figure 4-1). The only exception to this pattern was lodgepole pine roots which reached a maximum at 30 °C (Figure 4-1e). Combining all the species, the relative respiration rate of roots reached a maximum at 40 °C (Figure 4-1a).

4.4.2 Factors influencing Q_{10}

ANCOVA indicated that the Q_{10} of root respiration rate was influenced to a highly significantly degree ($P < 0.01$) by incubation temperature in the range of 5-40 °C, but not by species, decay class, or the direction of temperature change (Table 4-1). No significant impact of root moisture, a covariant in the analysis, was observed on the Q_{10} of woody roots. The Q_{10} of root respiration rate decreased with increasing temperature of incubation (Figure 4-2). For example, at 5 - 10 °C, Q_{10} averaged 3.99, decreased to 2.4 at 10 - 15 °C, and then further declined with increasing temperature. The Q_{10} of respiration rate of decomposing roots in temperature range 5 - 10 °C and 10 - 30 °C were significantly higher than those of the rest temperate ranges (Table 4-2). Regression analysis indicated Q_{10} of root respiration rate could be expressed by a single-exponential model:

$$Q_{10} = 4.31 * e^{(-0.036 * Temp)}$$

where Temp was temperature (° C). This model was significant ($P < 0.02$) and accounted for 77% of the variation of Q_{10}.

The direction of temperature change did not significantly influence Q_{10} of root respiration rate ($P = 0.54$), indicating hysteresis may not occur for the temperature range of 5 to 40 °C we examined (Table 4-1 and Table 4-2). However, the standard errors of Q_{10} were large in comparison to the mean Q10 values, especially on low incubation temperature such as 5-10 °C range (Table 4-2), suggesting better experimental design using more tightly constrained decomposing roots would be needed in the future to detect whether hysteresis really occurs or not with the direction of temperature change in root decomposition.

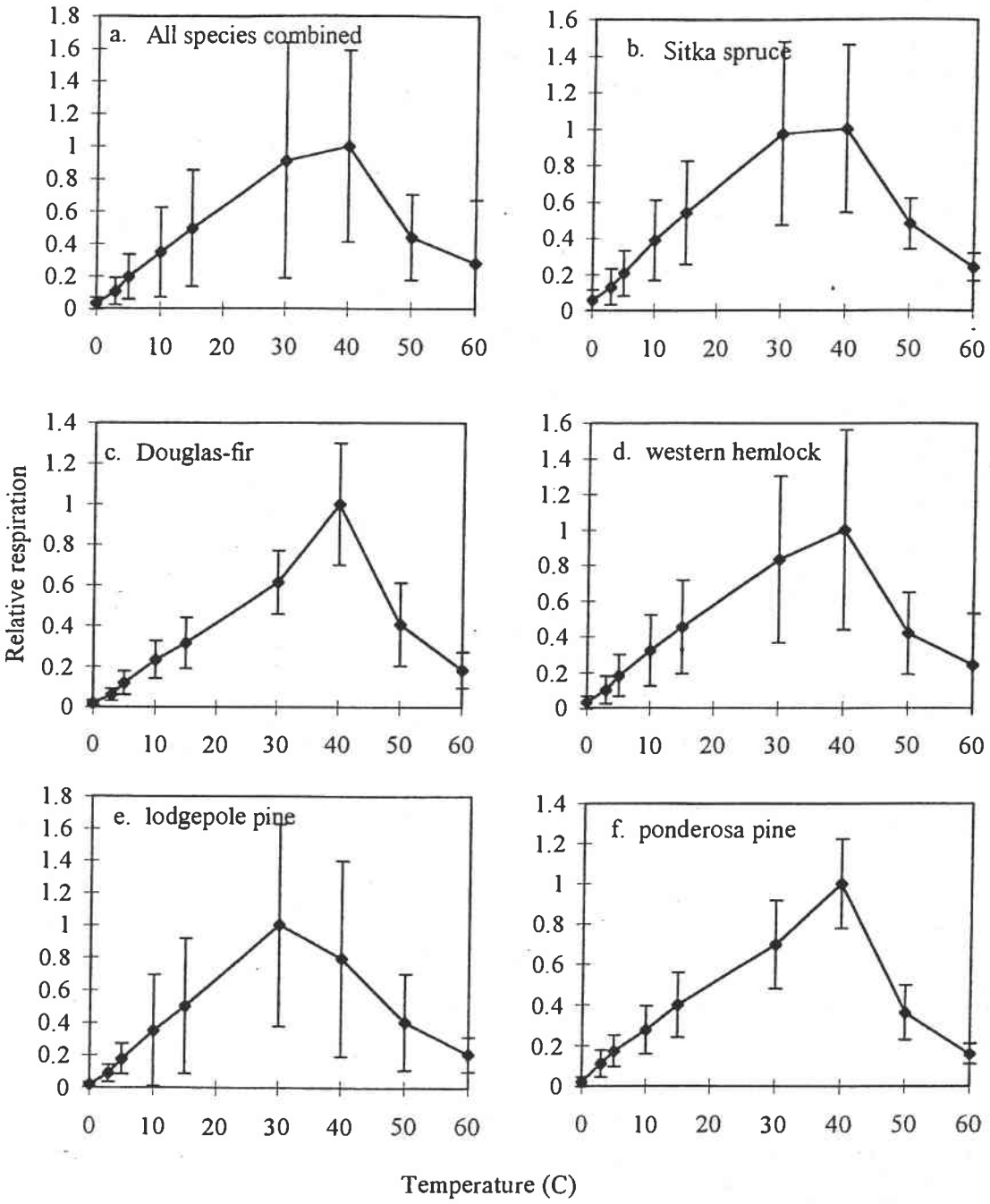

Figure 4-1. Relative respiration of decomposing roots incubated 4 hours at different temperatures*.

*: For individual species, n = 12 for temperature 0 - 40 ^{0}C and n = 6 for temperature 50-60 ^{0}C range.

*: For all species, n = 60 for temperature 0 - 40 ^{0}C and n = 30 for temperature 50-60 ^{0}C range.

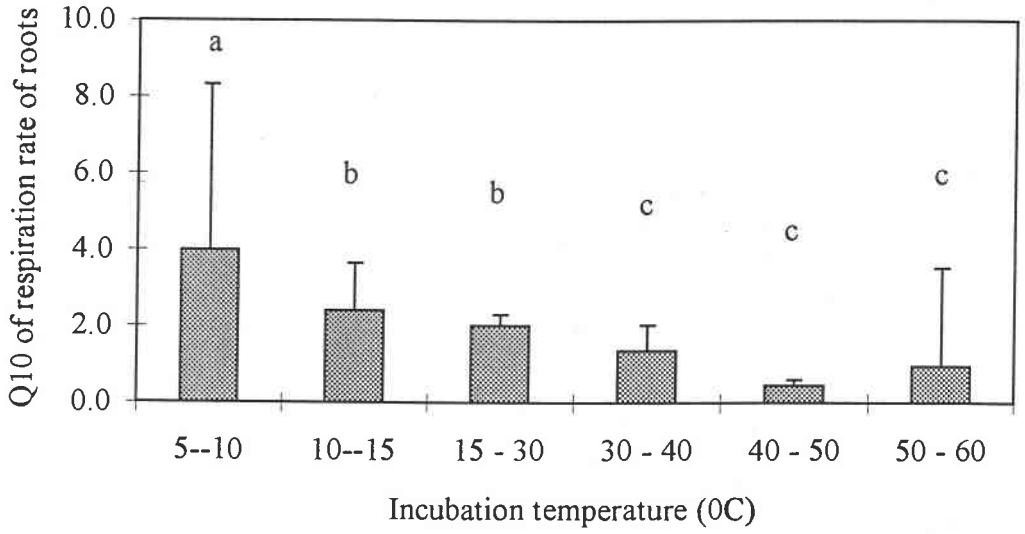

Figure 4-2. Q10 of respiration rate of decomposing roots for different ranges of incubation temperature*.

* Q_{10} value was calculated from 60 samples in each temperature range lower than 40 ^{0}C. Beyond 40 ^{0}C, each mean Q_{10} was calculated from 30 samples.
* Different letters indicate significant difference among the means ($P < 0.05$).

Table 4-1. ANCOVA results of factors influencing the Q_{10} of respiration rate of decomposing roots.

Source	df	Sum of Squares	Mean Square	F Value	*P* value
Temperature	3, 239	258.45	86.15	16.58	0.01
Species	4, 239	25.00	6.25	1.20	0.31
Decay class	2, 239	8.31	4.16	0.80	0.45
Direction	1, 239	1.92	1.92	0.37	0.54
Moisture (Covariate)	1, 239	1.00	1.76	0.34	0.56

Table 4-2. Impact of the direction of temperature change on the Q_{10} of respiration rate of decomposing roots*.

Direction	Temperature range (^{0} C)			
	5 -- 10	10 -- 15	15 -- 30	30 -- 40
Increase	3.70 (3.63)	2.18 (1.14)	2.10 (0.30)	1.40 (0.68)
Decrease	4.3 (5.12)	2.62 (1.36)	1.90 (1.25)	1.33 (0.68)
Mean	3.99 (4.34)	2.4 (1.24)	2.02 (0.58)	1.37 (0.68)

* : The values in parenthesis was one standard error.

4.4.3 Moisture effects

The relative respiration rate of roots increased with root moisture, reached a peak at an optimum moisture range, then decreased beyond that moisture, regardless of incubation temperatures (Figure 4-3). The exceptions to this pattern were Douglas-fir, ponderosa pine, Sitka spruce which continuously increased with increasing moisture. The optimum root moisture differed among species. For example, the optimum moisture range of lodgepole pine was between 125 to 225%. While the optimum moisture of Sitka spruce was wider, at least ranging from 125 to 275%, although we were not sure what would happen to the relative respiration rate when moisture was higher than 275%. When the moisture of woody roots was reduced to 20-50%, the relative respiration rate was very low for all five species examined.

Two-way Analysis of Variance (ANOVA) indicated that the respiration rate of decomposing roots was influenced to a highly significantly degree by root moisture and incubation temperature ($P < 0.01$), but not the direction of moisture change ($P = 0.14$). The interaction of temperature and moisture on root respiration rate was also highly significant ($P < 0.01$) (Table 4-3 and Figure 4-4). At a very low root moisture content, the effects of three different incubation temperatures were negligible, resulting in a very low respiration rate. Surprisingly the temperature effects from 5 to 15 °C observed in the moisture experiment were not similar to those occurred in the previous temperature experiment. In contrast, the responses of root respiration rate at 30 °C was consistent with the temperature experiment (Figure 4-4). The lack of influence of direction of root moisture change suggests that hysteresis effects did not occur.

4.4.4 Species and decay class effects

In addition to root moisture and incubation temperature, the respiration rate of decomposing roots was also highly significantly influenced by species and decay class ($P < 0.01$) (Table 4-3). Among the five species examined, lodgepole pine showed the highest respiration rate with a mean value of 17.2 $\mu g\ g^{-1}\ hr^{-1}$, western hemlock the second with a rate of 13.2 $\mu g\ g^{-1}\ hr^{-1}$, and Douglas-fir, ponderosa pine, and Sitka spruce were similar, ranging from 6.3 to 8.4 $\mu g\ g^{-1}\ hr^{-1}$ (Figure 4-5). Roots of decay

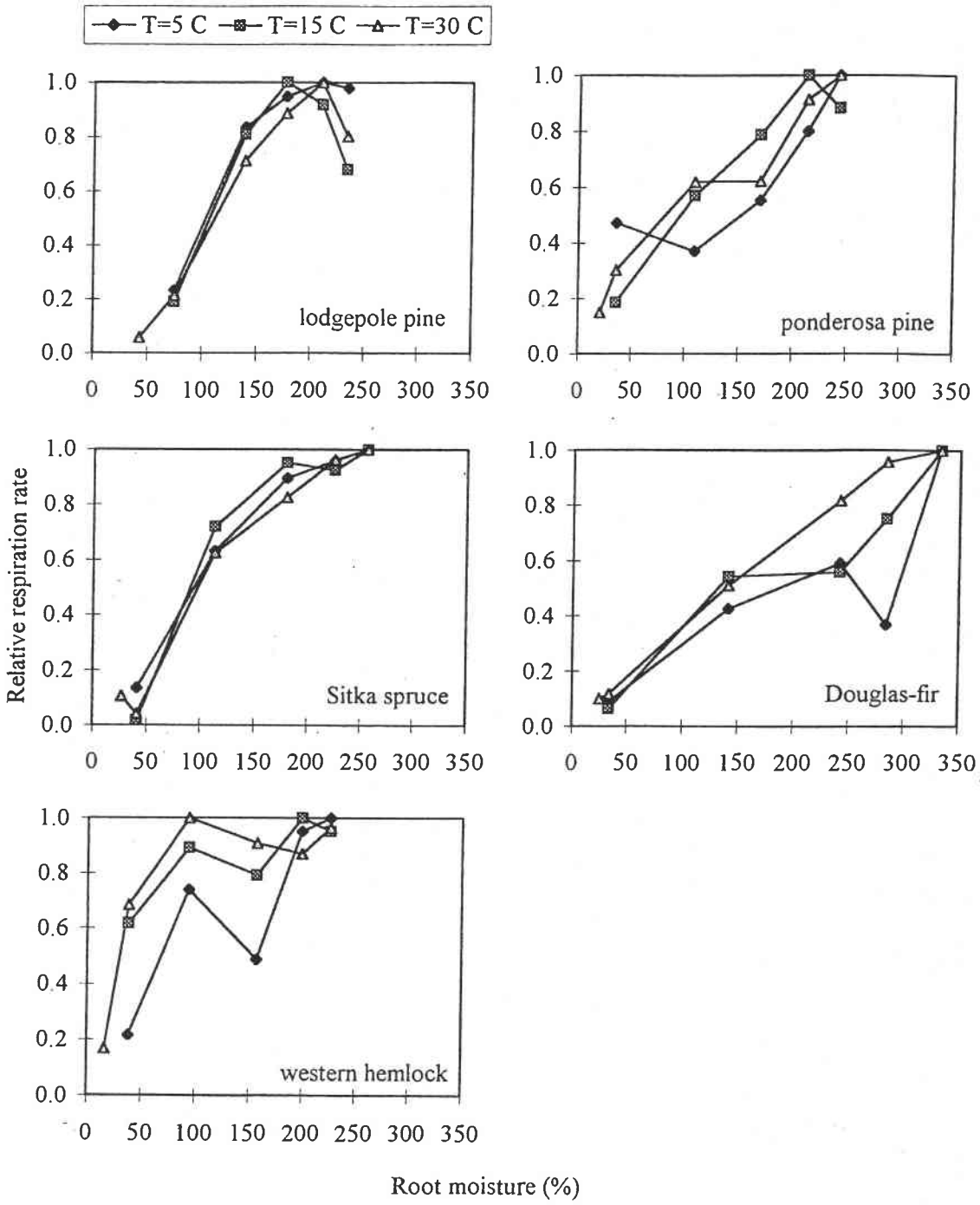

Figure 4-3. Relative respiration rate of decomposing roots under different moisture and temperatures*.

*: Each point is the mean of 6 samples which include three decay classes and two reps.

Table 4-3. ANOVA results of the factors influencing respiration rate of decomposing roots.

Source	df	Sum of Squares	Mean Square	F Value	*P* value
Moisture	5, 749	12985.04	2597.01	25.89	0.01
Temperature	2, 749	28442.29	14221.15	141.77	0.01
Moisture * Temperature	8, 749	2131.04	266.38	2.66	0.01
Species	4, 749	13260.46	3315.12	33.05	0.01
Decay class	2, 749	2900.11	1450.05	14.46	0.01
Direction	1, 749	216.09	216.09	2.15	0.14

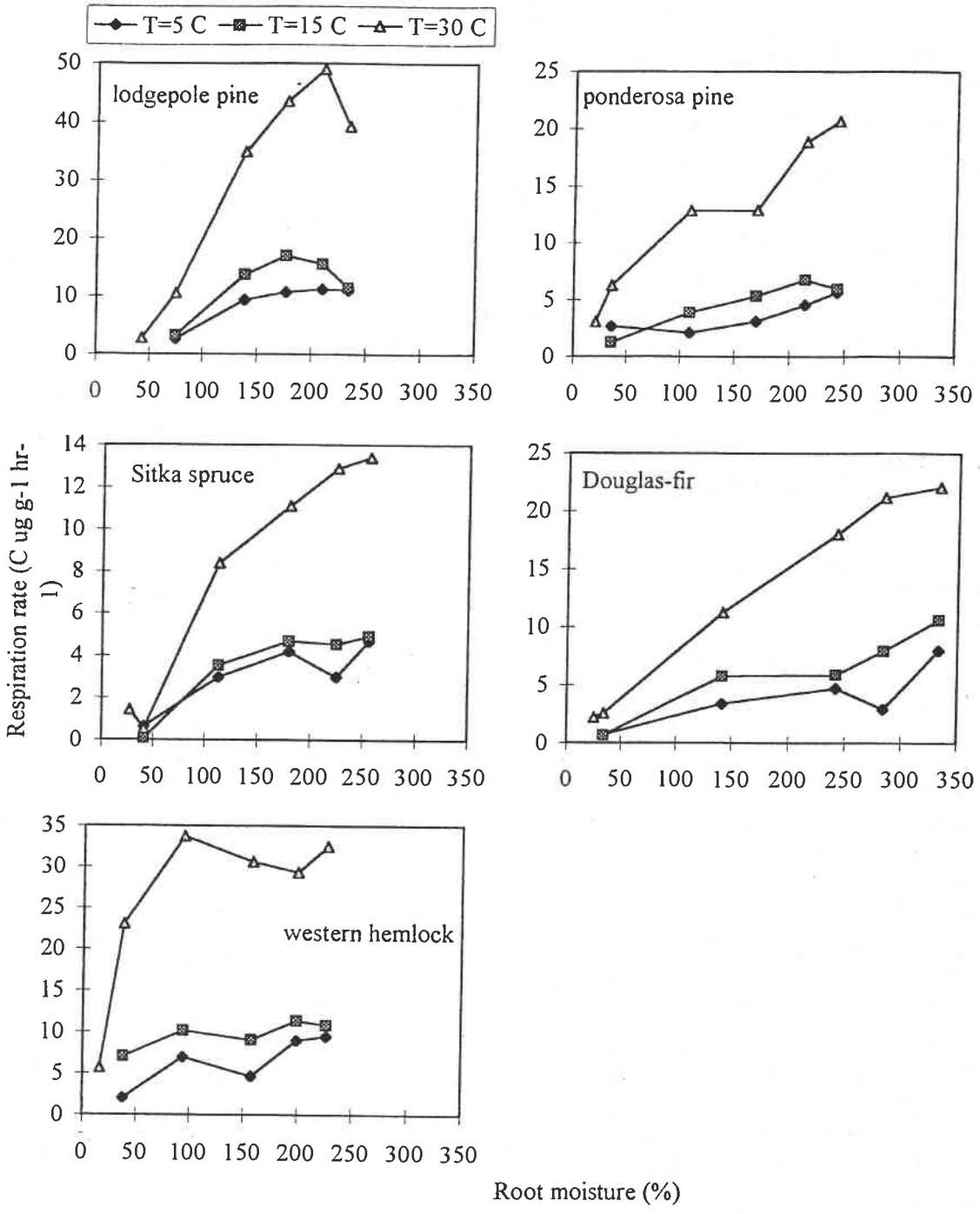

Figure 4-4. Respiration rate of decomposing roots under different moisture and temperatures*.

*: Each point is the mean of 6 samples which include three decay classes and two reps.

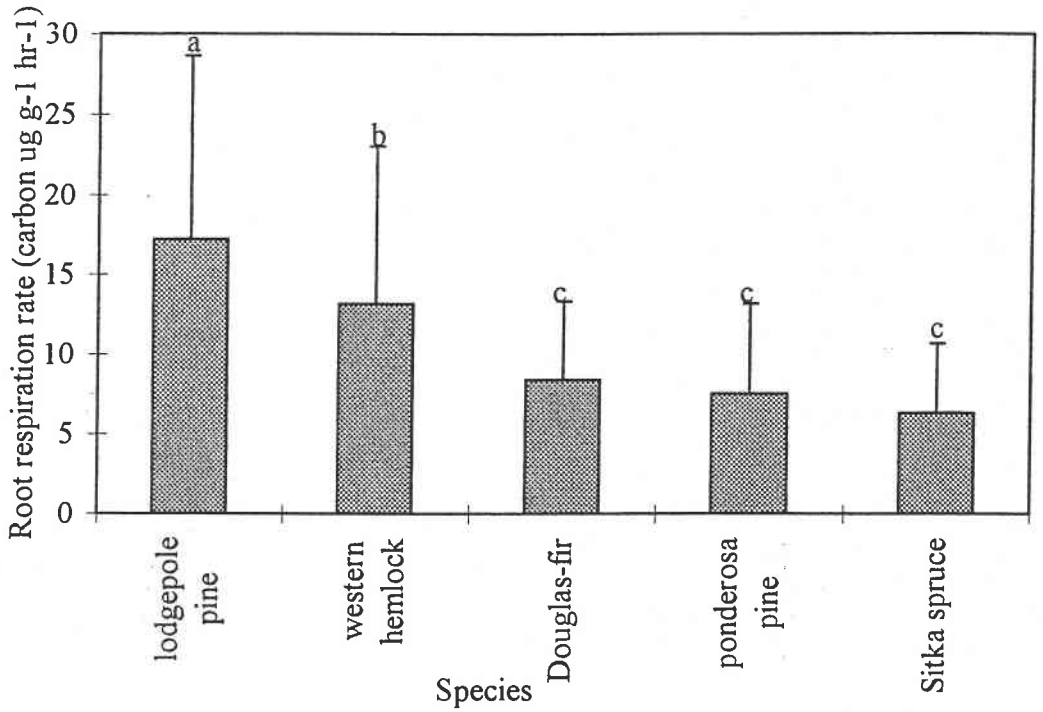

Figure 4-5. Species effects on respiration rate of decomposing woody roots*.

* Each mean value was calculated from 144 samples.
Different letters indicate significant difference among the means ($p < 0.05$).

class I and III had a significantly higher respiration rate than that of decay class II (Figure 4-6). The high standard error of respiration rate with Figures 4-5 and Figure 4-6 was mainly due to the fact that we had three temperature (5, 15, and 30 °C) treatments in this experiment.

4.5 DISCUSSION

4.5.1 Temperature effects

The general response of respiration of decomposing woody roots to temperature was very similar to those of aboveground litter: enhanced respiration with increasing temperatures up to an optimum temperature, and retarded respiration with temperature above that point (Boddy, 1983; Flanagan and Veum, 1974; Moore, 1986; O'Connell, 1990). Increasing temperature enhances the enzyme activities and hence respiration and enzymatic breakdown of polymers (McClaugherty and Links, 1990). Increasing of incubation temperature to 50 and 60 °C caused the respiration of roots to decline (Figure 4-1), although the respiration process did not stop completely. This decrease is probably due to the denaturing of decomposer proteins. These high temperatures may occur in clear-cut forest sites where high radiation inputs occur.

In our study, the optimum temperature was between 30 to 40 °C (Figure 4-1) which is consistent with the incubation results of deciduous forest-leaf and Douglas-fir fine litter (Moore, 1986) and litter of eucalyptus forests at Australia (O'Connell, 1990). Moore (1986) indicated the decomposition rates of deciduous forest leaf sampled at North Carolina and Douglas-fir needles collected at HJA approached a maximum near 40 °C. Similarly, O'Connell (1990) found the optimum temperature for respiration of litter of eucalyptus forests was 33-34 °C. However, Flanagan and Veum (1974) found the optimum temperature of organic residues from the Alaska Tundra was 25 °C. This low optimum temperature may be due to the decomposers of this tundra region which might be adapted to cold climate. The similarity of temperature responses in temperate forests regardless of sampling season and site (this study and Moore, 1986) may indicate that the decomposer groups from the same climatic zone may be similar. Our

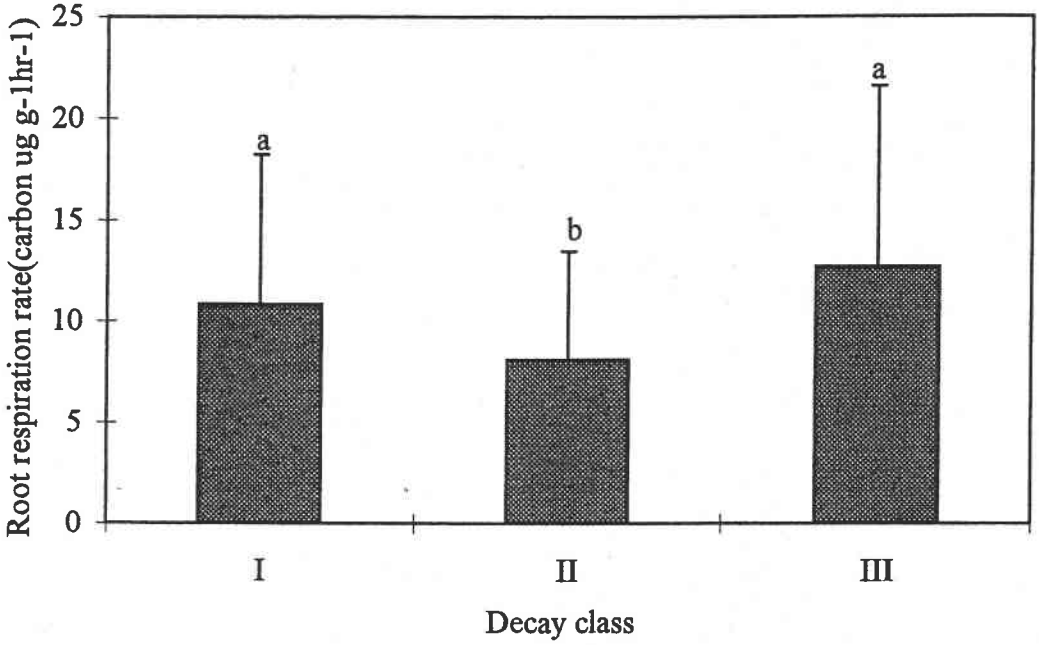

Figure 4-6. Decay class effects on respiration rate of decomposing roots*.

* Each mean value was calculated from 270 samples.
Different letters indicate significant difference among the means ($p < 0.05$).

preliminary laboratory incubation of decomposing root samples collected in the spring of 1996 from the same three stands at each site also showed an optimum temperature between 30 - 40 °C (Chen and Harmon, unpublished data).

The Q_{10} of respiration rate of decomposing roots was significantly influenced by temperature being greater at low (Q_{10} = 3.99, 5-10 °C) than at moderate (Q_{10} = 2 ~ 2.4,10-30 °C) or high (Q_{10} = 0.46 ~ 1.37, 30 - 60 °C) temperature (Figure 4-2). The high Q_{10} values at low temperature indicate positive temperature effects on enzyme activities. In contrast, the low Q_{10} value at high temperature is due to increased enzyme denaturing. The Q_{10} pattern of decomposing roots was similar to those of soil organic matter (De Jong et al., 1974; Kirschbaum, 1995; Raich and Schlesinger, 1992; Winckler et al., 1996). Kirschbaum (1995) indicated Q_{10} of soil organic matter decreased from almost 8 at 0 °C to about 4.5 at 10 °C and 2.5 at 20 °C. Winckler et al. (1996) calculated that Q_{10} of A horizon soil of a temperate forest at North Carolina varied from 1.9 to 1.7 over the temperature range of 4 to 28 °C. Raich and Schlesinger (1992) compiled literature values from year - round field studies and calculated an average Q_{10} of 2.4. Q_{10} values between 1.6 and 3.7 have been recorded for microbial respiration for many temperate and tropical systems over a temperature range between 10 and 40 °C (Anderson, 1992; Schlesinger, 1977; Singh and Gutpka, 1977).

Species, decay class, and moisture of dead roots did not show a significant influence on Q_{10} as we had expected. We would expect that species with higher substrate quality should be more responsive to changes in temperature. This suggests that the relative activities of root decomposer may be influenced more by abiotic factors such as temperature than biotic factors such as species and decay class. The lack of significant moisture effect on Q_{10} observed in this study is mainly due to the fact that most moisture contents of the samples incubated were between 100 - 240%, a moisture range favorable for microbial respiration.

4.5.2 Moisture effects

Both extremely low and high moisture contents can limit the activity of decomposer organisms. In our study, below 30% moisture content (the fiber saturation

point), water was generally not available for metabolic activity of microbes. This result is similar to the other studies (Boddy, 1983; Griffin, 1977). Increasing moisture content enhanced respiration of roots until an optimum moisture range was reached. This optimum moisture content ranged between 100 to 275% depending on the species in our study. When root moisture was above the optimum range excess moisture probably retarded decomposition by reducing the diffusion rate of oxygen (Killham, 1994). High moisture limitation on root respiration was not observed in Sitka spruce, Douglas-fir and ponderosa pine (Figure 4-3). This is may be due to a lack of water saturation in these species. A soaking period of more than 5 days may be needed to create saturated moisture contents.

The interaction of temperature and moisture on respiration of dead roots differed depending on the moisture content of woody roots (Figure 4-4). At low moisture contents (< 75% of dry weight) temperature increases had little effect on respiration, but at higher moisture contents (100-200%), respiration was more responsive to temperature increases, especially in a temperature range of 15 °C to 30 °C. Our results were very similar to those of Schlenter and Van Cleve (1985), who examined abiotic controls on soil respiration.

4.5.3 Short-term incubation versus long-term decomposition

Our main purpose in this study was to understand how the change of temperature and moisture influence the response of respiration of decomposing roots, but not to measure the exact respiration rate of decomposing roots. Qualitatively, root respiration was significantly influenced by species, decay class, root moisture, and incubation temperature observed in this short-term laboratory incubation study (Table 4-3), which is consistent with the results of most field root decomposition studies (Camire et al., 1991; Fahey et al., 1988; McClaugherty et al., 1984). However, we are cautious about long-term mass-loss extrapolations based on these short-term laboratory incubation results. Long-term root decomposition study in field sites is necessary to validate our respiration data. Nevertheless, the short-term laboratory incubation

approach provided a good way to examine factors controlling root decomposition and how these factors vary across their range in a relative sense.

4.5.4 Implications for global climate change modeling on root carbon flux

Soils are of particular importance in the atmospheric CO_2 budget. Soil organic matter contains a large reservoir of carbon, recently estimated at ~1600 Pg, more than twice the atmospheric carbon pool (Jenkinson et al., 1991; Raich and Potter, 1995). Dead roots are an important carbon pool in soil, accounting for up to one-third of total soil respiration in temperate soils (Bowden et al., 1993). Therefore an increase in the CO_2 flux from this pool in response to global climate warming will have a major influence on atmospheric CO_2 concentrations. A simple constant of $Q_{10} = 2$ has been widely used in modeling temperature effects on carbon release from soil organic matter and other organic detritus, regardless of temperature conditions (Potter et al., 1993; Raich et al., 1991). Our study indicated that Q_{10} of respiration rate of decomposing roots decreased exponentially with increasing temperature. Similar changes in Q_{10} with temperature were observed in several soil organic matter studies (De Jong et al., 1974; Kirschbaum, 1995; Schlenter and Van Cleve, 1985; Winckler et al., 1996). A simple example illustrates the importance of using an appropriate Q_{10}. Assuming the annual temperature at PRF increases due to global climate warming to 10.7° C from a current mean temperature of 5.7°C, the carbon flux of dead roots will double if the Q_{10} of 4 (based on our laboratory study result) is used. In contrast, if the traditional Q_{10} of 2 is used the carbon flux of dead will increase only 1.4 fold. Therefore varying the Q_{10} from 2 and 4 would result in a 60% difference in the carbon flux from roots. The modeling of climate warming effects on forest root carbon flux should consider to use a temperature dependent Q_{10} value in their models.

4.6 CONCLUSIONS

The respiration of dead roots increased with temperature and reached a maximum at 30- 40 °C, and then decreased. The Q_{10} of respiration rate of dead roots was significantly influenced ($P < 0.01$) by temperature, but not by species, decay class,

and the direction of change. At 5 - 10 °C, Q_{10} averaged 3.99 and then decreased to 1.37 at 30 to 40 °C. Over a range of 5 - 60 °C, Q_{10} could be predicted by a single-exponential model using temperature as the independent variable. The respiration rate of decomposing roots was influenced to a highly significantly degree by root moisture, species, and decay class. The optimum root moisture ranged from 100 to 275% depending on the species. When roots were too dry (< 50%) or too wet (> 300%) root moisture became a limiting factor. Moreover, there were apparent interactions of root moisture and temperature on root respiration. Our study showed the direction of temperature and moisture change did not influence root respiration, indicating hysteresis may not occur for either the temperature or the moisture ranges we examined. The modeling of global climate warming effects on forest root carbon flux should consider a temperature dependent Q_{10} value. The short-term laboratory incubation approach provided a good way to examine temperature and moisture controls on root decomposition, although we are cautious about long-term mass-loss extrapolations based on these short-term results.

4.7 ACKNOWLEDGEMENTS

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CHAPTER 5

MOISTURE DYNAMICS OF DEAD ROOTS IN SOILS: A PRELIMINARY LABORATORY STUDY

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5.1 ABSTRACT

Two laboratory experiments were conducted to explore how species, root size, and soil moisture influenced moisture dynamics of dead roots in soils. In the wet root experiment, a series of different sized, water saturated Douglas-fir and western hemlock roots (0-20 mm) were buried in dry soils for two months. Root gravimetric moisture content decreased over the incubation time, regardless of species and root size. Moisture of smaller roots decreased faster than that of larger roots. In the dry root experiment, dry Douglas-fir and ponderosa pine roots were buried in very wet soils for ~ 2 months. The moisture content of these roots initially increased rapidly and then gradually reached a steady-state, regardless of species and root size. Moisture of smaller size roots increased faster than those of larger size roots for both species in wet soils. A simple diffusion model with two parameters was used to fit changes of root moisture of both experiments. Experimental and model parameters both indicated that the dead roots gained water faster than they lost moisture in soils. The diffusion model successfully simulated dead fine root moisture dynamics under field conditions, although more studies using different root species, decay class roots, and soil texture should improve its application to other sites.

5.2 INTRODUCTION

Moisture is important in controlling woody detritus decomposition (Griffin, 1977; Harmon et al., 1986). Suitable moisture conditions of soil and dead roots enhance the activities of soil decomposer organisms and thus increase root decomposition (see Chapter 4). To predict root decomposition correctly it is therefore important to understand factors controlling dead root moisture dynamics. Soil moisture directly influences the moisture level of dead roots in soils by the process of diffusion (Jury et al., 1991). Soil moisture can be successfully predicted by radiation, soil physical properties, and the characteristics of vegetation such as leaf area index and water use efficiency (Rosenberg, 1974; Monteith and Unsworth, 1990). Although a strong relationship between root moisture and soil moisture is assumed in many models, this relationship becomes complex with increasing root size due to decreasing

diffusion rates and increasing time-lags. In theory, the rate of moisture diffusion between roots and soils is controlled by dead root physical properties such as surface: volume ratio, decay class, density, and species as well as the moisture difference of both substrates. Unfortunately, how these physical features of dead roots actually influence root moisture in soils is unknown.

In this study, we conducted two laboratory experimental studies to explore how soil moisture influences the moisture of dead roots of different species and size. In the wet root experiment, water saturated roots of different size were placed in dry soils. In the dry root experiment, dry roots of different size were buried in very wet soils. These two conditions were selected as they represented the extreme cases of root moisture in soils.

5.3 MATERIALS AND METHODS

5.3.1 Soils and roots

The forest soils used in the laboratory studies were from a Douglas-fir (*Pseudotsuga menziensii*) old-growth forest at H. J. Andrews Experimental Forests (HJA). HJA is located 80 km east of Eugene, Oregon on the west slope of the Cascade Range. The climate is maritime, with wet, relatively mild winters and dry, cool summers. Mean annual temperature is 8.5 °C and mean annual precipitation is 2300 mm. The forests are classified into two major zones, the western hemlock (*Tsuga heterophylla*) zone (300-1550 m elevation) and the Pacific silver fir zone (1050-1550 m elevation). Douglas-fir and western red cedar (*Thuja plicata*) are also major components of both zones (Franklin and Dyrness, 1973). Soils at this site are deep, well-drained typic dystrochrepts; slope gradient ranges from 20-60%. Bulk density of the top 20 cm mineral soils averaged 0.55 g/cm^3 (one standard error = 0.12 g/cm^3, n = 17) (Remillard, unpublished data). The soils used in these experiments were collected from the top 0 - 20 cm mineral soil horizon. Mineral soils were collected in November of 1994 and were transported to the laboratory at Corvallis. Litter, living and dead roots, and large rocks (> 1 cm) were first sorted out from the soil. Next, the sorted

soils were completely mixed and the homogenous soils were then put 12 buckets (20 cm diameter x 50 cm height) until each bucket was two-thirds full. The remaining soils were stored for future needs.

Fresh woody roots of Douglas-fir and western hemlock were collected from recently uprooted trees caused by windthrow or road building at HJA. In addition, fresh ponderosa pine (*Pinus ponderosa*) woody roots were obtained from recently uprooted trees at Pringle Falls Experimental Forests (PRF) in central Oregon (see Chapter 2 for detail description of PRF). These woody roots were first cleared of surface soil, then they were sorted into fine (< 3 mm), small (4-8 mm), medium (10 - 13 mm), and large roots (> 15 - 20 mm). All roots except for fine roots were cut into 10 - 15 cm long segments that were air-dried at room temperature to a constant mass (20-50 days). Each piece of woody root was then tagged with a unique numbered aluminum tag indicating the species and size class.

5.3.2 Moisture experiments

Two experiments of soil-root moisture exchange were conducted in our laboratory at a room temperature of 19 °C. Each experiment included two species and four size classes of roots. Eight root samples of known moisture content (2 species X 4 size roots) were buried in the soil of each bucket. To reduce soil contamination and aid recovery, buried roots were covered by mesh (mesh size = 0.4 mm). Each bucket was tightly covered by a lid during the incubation period. Over a 2-month period, buried roots were sampled 6 times. Two buckets were randomly selected for each harvest from a total of 12 initial buckets. After each harvest, woody roots were first cleared of surface soil. Then they were dried to a constant mass at 65 °C and weighed after their initial wet weights were recorded. Finally the gravimetric moisture content of root sample was calculated based on water weight divided by dry weight.

The wet root experiment was designed to explore how moisture of wet dead roots changed over time in dry soils. It was conducted in November and December of 1994. Freshly dead roots of Douglas-fir and western hemlock were soaked in water for one week to reach a high moisture content. For each root type, initial gravimetric

moisture content of three samples were measured. The average moisture content of these three samples served as the initial gravimetric moisture content. Soils were air-dried at 17 °C room temperature for one week. Soil gravimetric content of each bucket was measured and the average soil moisture content of 12 buckets was 23.2% (se = 1.2%). During 2 months, buried roots were sampled after 5, 10, 20, 30, 45, and 60 days. Root moisture content was measured after each harvest as described above.

The objective of the dry root experiment was to monitor how moisture of dry dead roots changed over time in wet soils. The experiment was conducted in March and April of 1995. The moisture contents of initial air-dried roots ranged from 6.2 to 11.8% prior to the experiment. Due to the lack of medium size roots of ponderosa pine only three size roots of this species were included in this experiment. The same soils from the wet root experiment were used. Field moisture capacity was reached by pouring water into each bucket. The final average soil moisture content was 52.7% (se = 1.1%). During the experimental period, buried roots were sampled after 5, 12, 22, 35, 49, and 67 days. Root moisture content of each sample was measured as described above.

5.3.3 Moisture measurements of fine roots and soils under field sites

Fine root moistures were measured at the Cascade Head, H. J. Andrews, and Pringle Falls Experimental Forest sites every six month. The seasonally dynamics of soil moisture at the three sites were measured using Time Domain Reflectometry (TDR) (see Chapter 3 for the details).

5.3.4 Data analysis

A simple diffusion model was used to fit the moisture data of both experiments. The model used to describe the diffusion process of moisture exchange between roots and surrounding soils was:

$$\Delta M_{t\_roots} = k_1 * [M_{soils} - (k_2 * M_{(t-1)\_roots})]$$

where M_{t_roots} and $M_{(t-1)\_roots}$ are root gravimetric moisture content at time t and t-1 days since the incubation, respectively; ΔM_{t_roots} is daily rate of change of root moisture, and

M_{soils} is the soil moisture content. The parameter k_1 indicates how fast moisture diffusion (exchange) occurs between roots and soils, while parameter k_2 describes the asymptote when moisture exchange of roots and soils reaches a steady-state. Parameter k_1 and k_2 were determined by least-squares regression (Jongman et al., 1995).

An assumption of this model was that the change of incubated root moisture did not influence the moisture of surrounding soils (M_{soils}) over the laboratory incubation period. This assumption was reasonable given the relatively small amount of roots incubated compared to the soils in each bucket. Periodical soil moisture measurements of each bucket confirmed the assumption that M_{soils} was constant.

5.4 RESULTS

5.4.1 Wet roots in dry soils

Root gravimetric moisture decreased rapidly during the initial stages and then gradually reached a steady-state, regardless of species and root size (Figure 5-1). In addition, the moisture of smaller sized roots of Douglas-fir decreased faster than those of larger roots. For example, fine root moisture of Douglas-fir decreased from an initial 97% to 26.9% in first 5 days, then fluctuated around a steady-state moisture level of 25% over the remaining 55 days of incubation. In contrast, the moisture of Douglas-fir small, medium, large roots decreased from 111%, 102%, 87% to 70-80% for the same period, and continued to decrease until reaching a common steady-state moisture content of 40% after 30 days of incubation.

The effect of root size on the drying of wet western hemlock roots in dry soils was not as apparent as for Douglas-fir. In the first 5 days of incubation, moisture of fine, small, and medium western hemlock roots lost almost half of their initial moisture contents, regardless of size (Figure 5-1). However, for the same period, the large roots of western hemlock only lost one-quarter of their initial moisture, indicating the occurrence of a size effect (Figure 5-1). The final steady-state moisture content of

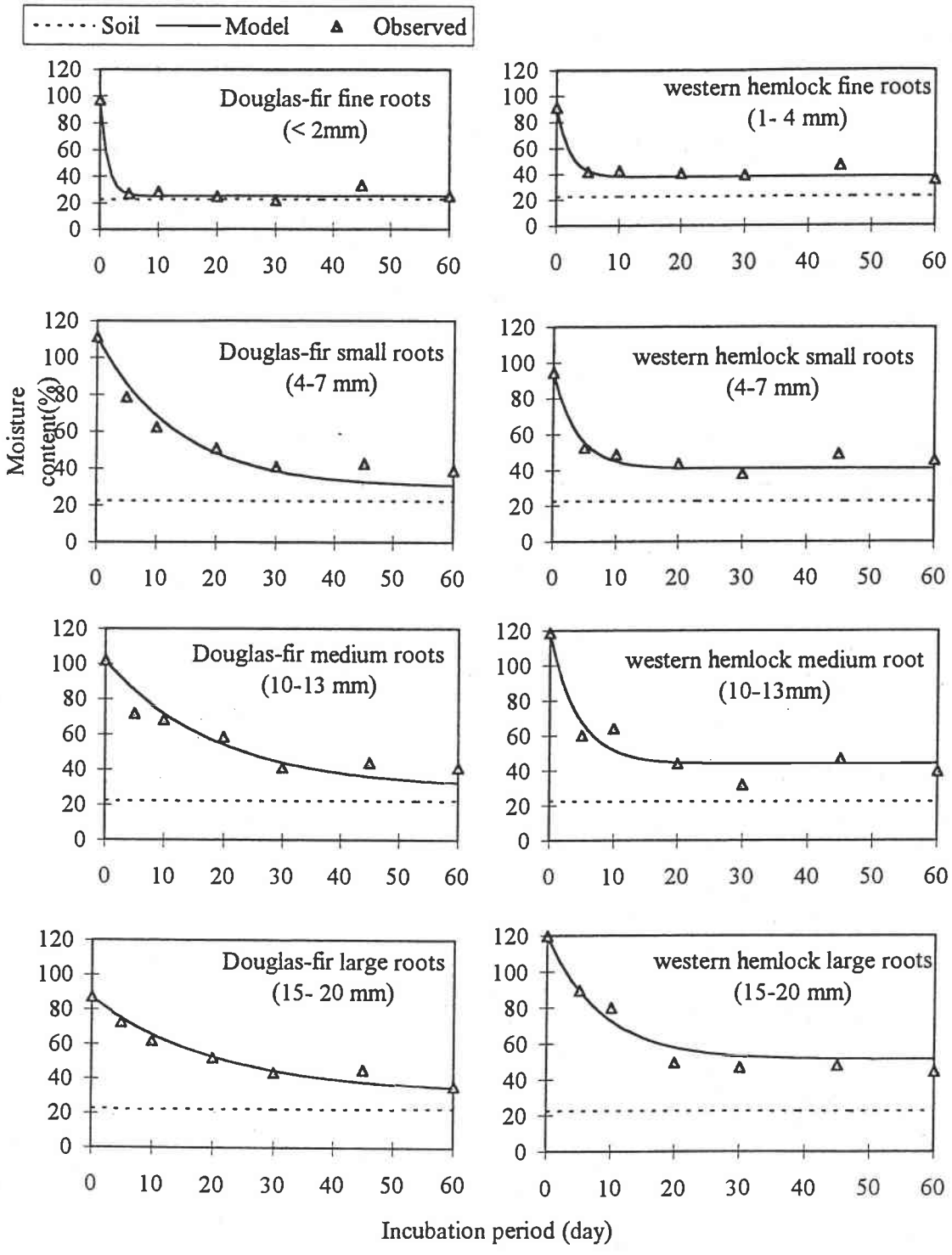

Figure 5-1: Changes in moisture content of wet dead roots in dry soil.

western hemlock roots was similar to those of Douglas-fir, ranging from 36% to 46%. The diffusion model fit the moisture data of different size roots very well (Figure 1 and Table 5-1), with the coefficient of determination of the regressions generally over 0.92. The only exception to this was the medium roots of Douglas-fir with a R^2 of 0.89. Both model parameters, k_1 and k_2, decreased with increasing root size, regardless of species (Table 5-1). For example, k_1 decreased from 0.63 for western hemlock fine roots to 0.25 for large roots. As k_1 decreases, decomposing roots lose moisture slower. The decrease of k_2 with size denotes the difference between soil moisture and steady-state root moisture increases.

5.4.2 Dry roots in wet soils

The gravimetric moisture of dry roots buried in mineral soils at field capacity rapidly increased initially and then gradually reached a steady-state level over time, regardless of species and root size (Figure 5-2). After 5 days moisture of Douglas-fir roots increased to about 40-90%. In the next 5 days, the root moisture of Douglas-fir only increased 10-20% except the large roots which had increases similar to the first 5 days. In general, moisture of Douglas-fir roots reached a steady-state of 80-130% after 12 days of incubation. A similar pattern was observed in ponderosa pine roots. In the initial 12 days of incubation, root moisture increased 90-140%, and then fluctuated near 160%, 120%, and 110%, for fine, small, and large roots, respectively.

Moisture of smaller size roots increased faster than those of larger size roots for both Douglas-fir and ponderosa pine in wet soils (Figure 5-2). In addition, smaller roots reached a higher steady-state moisture content than larger roots (Figure 5-2). For example, moisture of Douglas-fir fine roots increased from 12% to 138% over 67 days. In contrast, Douglas-fir large roots increased from 6% to 75.2% in the same period. Similarly, fine root moisture content of ponderosa pine increased from 8% to 207% in 67 days in comparison to 6 to 110% for large roots.

The diffusion model closely fit the rewetting process of dry roots in wet soils (Figure 5-2 and Table 5-1), explaining more than 88% of the data variation (Table 5-1). The parameter k_1 in the model tended to decreased with increasing root size of

Table 5-1. Parameters for dead root moisture dynamic model in dry and wet soils.

Species	Root diameter	Number	Regression coefficients[1]		R^2
			k_1	k_2	
Experiment one: wet roots in dry soils					
Douglas-fir	Fine roots (< 2mm)	7	0.590	0.900	0.98
	Small roots (4-7 mm)	7	0.096	0.750	0.94
	Medium roots (10-13 mm)	7	0.070	0.750	0.89
	Large roots (15-20 mm)	7	0.068	0.700	0.96
western hemlock	Fine roots (< 4 mm)	7	0.630	0.600	0.95
	Small roots (4-7 mm)	7	0.420	0.550	0.94
	Medium roots (10-13 mm)	7	0.400	0.510	0.92
	Large roots (15-20 mm)	7	0.250	0.440	0.95
Experiment two: dry roots in wet soils					
Douglas-fir	Fine roots (2-4 mm)	7	0.560	0.400	0.98
	Small roots (4-8 mm)	7	0.760	0.450	0.92
	Medium roots (10-12 mm)	7	0.460	0.500	0.88
	Large roots (24-35 mm)	7	0.230	0.650	0.98
ponderosa pine	Fine roots (2-5 mm)	7	0.470	0.283	0.89
	Small roots (7-8 mm)	7	0.450	0.420	0.95
	Large roots (14-20 mm)	7	0.550	0.470	0.93

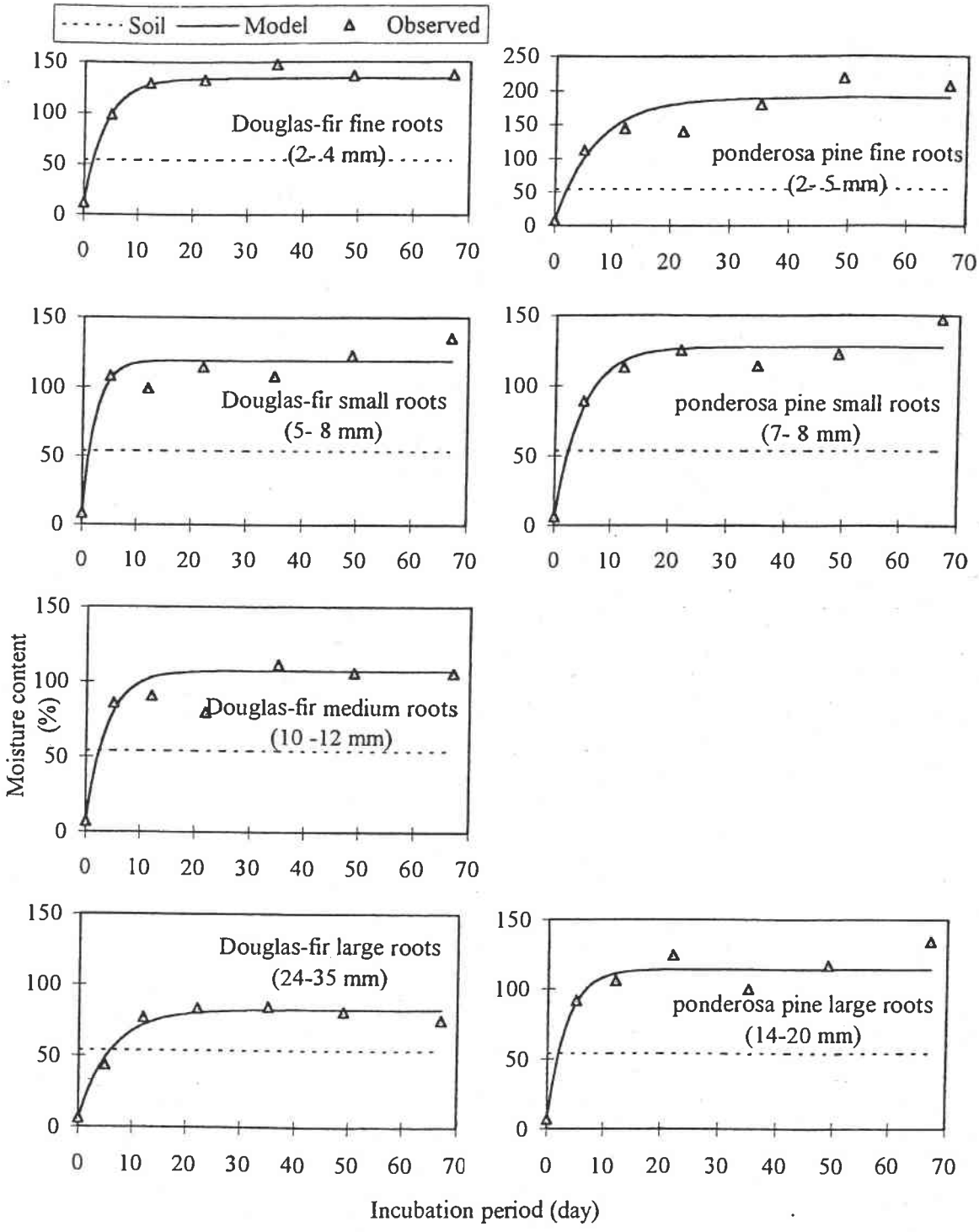

Figure 5-2: Changes in moisture content of dry dead roots in wet soil.

Douglas-fir (Table 5-1), suggesting small roots absorb soil moisture faster than large roots. The exception to this was ponderosa pine in which the parameter k_1 of different size roots were close (Table 5-1). Regardless of species, the parameter k_2 increased with increasing root size (Table 5-1), indicating that the difference between soil moisture and steady-state root moisture decreases with increasing root size.

5.4.3 Model predictions of fine root moistures under field conditions

The diffusion model was used to simulate long-term fine root moisture dynamics by replacing M_{soils} with TDR measured soil moisture data. In comparison to the observed moistures, the model predictions of fine root moistures were reasonably good for western hemlock, Douglas-fir, and ponderosa pine at Cascade Head, H. J. Andrews, and Pringle Falls Experiment Forest sites, respectively, although the model overestimated the root moisture of western hemlock and ponderosa pine in early June of 1997 (Figure 5-3). The model performance should be further improved if better resolution soil moisture data is used.

5.5 DISCUSSION

5.5.1 Factors controlling root moisture change in soils

Water movement in soil usually falls into three general categories: diffusion, active transport, and fluid flow (Jury et al., 1991). Active transport probably never occurs in dead root moisture exchange, although fungal hyphae may play a minor role. Fluid flow is unlikely in soils except when rainfall or snowmelt rates are high. Thus, diffusion is probably the dominant process in regulating moisture change of dead roots in soils. The rate of diffusion is controlled mainly by physical features such as root size, density, and differences between root and soil moisture content (Jury et al., 1991). Root size directly influences the surface area:volume ratio, increasing with decreasing root size. A high surface area:volume ratio enhances moisture diffusion as indicated by the decreasing value of k_1 as root diameter increased. Although these differences could also have been caused by differences in the initial root moisture contents these were

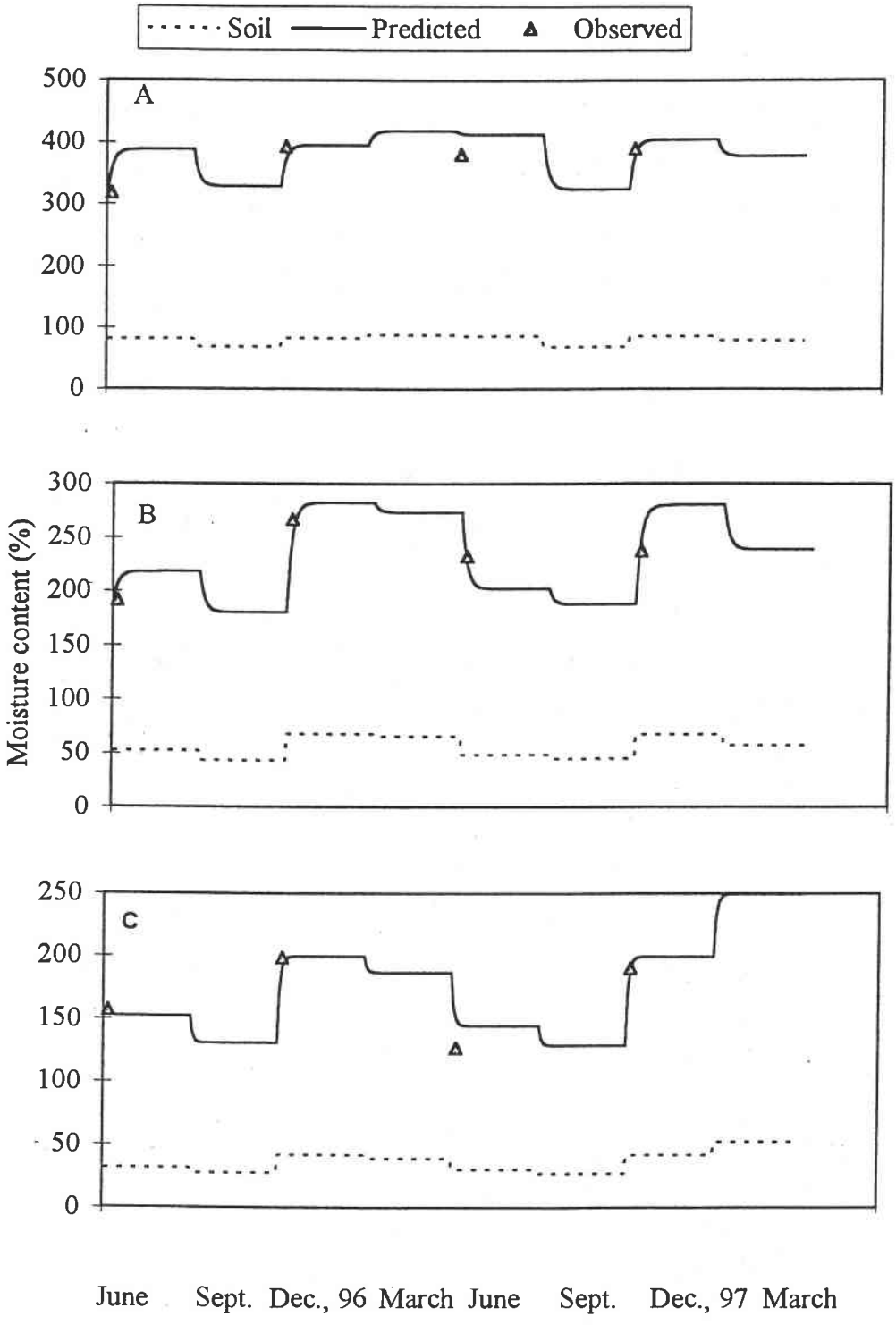

Figure 5-3. Moisture of fine roots changes over seasons at three sites: A. western hemlock at Cascade Head site; B. Douglas-fir at H. J. Andrews site, and C. ponderosa pine at Pringle Falls site.

minor in our experiment (Figure 5-1 and Figure 5-2). The smaller effect of size in western hemlock roots was probably due to the small size difference between fine and small roots (Figure 5-1 and Table 5-1).

Root density of dead roots should influence the capability of roots to uptake, store, and hold water. As density decreases the capacity of wood to store water increases (Peck, 1953; Harmon and Sexton, 1995). Since root density for a species did not change very much over size, density was not an important factor in our experiments. However, different densities for various species may result in different steady-state root moistures. For example, the fine root moisture content of ponderosa pine in our dry root experiment was obviously higher than that of Douglas-fir, which may reflect the lower density of the former species (0.35 g/cm^3 versus 0.45 g/cm^3). Root decomposition decreases root density over time and this should influence the maximum water content in woody roots.

Roots generally gained moisture faster than they dried (Figure 5-1 and Figure 5-2). Dry roots of Douglas-fir reached maximum moisture in wet soils in less than 22 days of incubation (Figure 5-2). In contrast, wet roots of Douglas-fir took 30 days in dry soils to reach a steady-state moisture level except for fine roots. This is evident in the change of parameter k_1 values for Douglas-fir roots under two experiments (Table 5-1) with a higher value in the dry root experiment than the wet root experiment. This suggests roots gain moisture faster than they lose it. This may be due to the root substrate structure and anatomy, although the exact reasons need to be explored further.

5.5.2 Model performance and implications

The diffusion model fit the root moisture change data well in our laboratory study, explaining more than 90% of the variation of the laboratory data (Table 5-1). Furthermore, the model has important implications for predicting root moisture dynamics based on soil moisture contents under field conditions. The model predictions of fine root moistures at the three sites were generally good, suggesting this

diffusion model has the potentials to simulate other woody root moisture contents under field conditions. The model therefore appears to be promising provided more studies using different root species, decay class, and soil textures are conducted in future.

5.6 CONCLUSIONS

Gravimetric moisture of wet roots decreased over time in dry soils, regardless of species, with smaller size roots decreasing faster than larger size roots. Gravimetric moisture of dry roots initially increased rapidly and then gradually reached a steady-state over time in wet soils, regardless of species. Moisture of smaller size roots increased faster than those of larger size roots for both species in wet soils. A simple diffusion model with two parameters was used to fit the root moisture changes of both experiments. The model performed well in matching the root moisture in the experiments with a R^2 of > 0.9. The experiments and model parameters indicated that the dead roots gained water faster than they lost it in soils. The diffusion model was favorably tested against field data which indicates it has utility for simulating dead root moisture dynamics under field conditions, although more studies using different root species, decay class, and soil textures are needed in future.

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CHAPTER 6

MODELING THE EFFECTS OF SUBSTRATE QUALITY, TEMPERATURE, AND MOISTURE ON ROOT DECOMPOSITION: IMPLICATIONS FOR CLIMATE CHANGE

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6.1 ABSTRACT

A root decomposition simulation model (ROOTDK) was developed to examine the effects of substrate quality, temperature, and moisture on woody root decomposition at three coniferous forests in the Pacific Northwest. Decomposition of woody roots of Sitka spruce and western hemlock at Cascade Head (CAH), Douglas-fir and western hemlock at H. J. Andrews (HJA), ponderosa pine and lodgepole pine at Pringle Falls (PRF) was simulated under current climate conditions. Douglas-fir was used to test the impacts of four climate change scenarios on root decomposition at the three sites. The model captured the overall mass loss pattern of Sitka spruce, Douglas-fir, and western hemlock at HJA under the current climate. After 30 years of decomposition, the ROOTDK model predicted that Sitka spruce, Douglas-fir, and western hemlock (at HJA) lost 51, 42, 61% of initial mass in comparison to 50, 32, and 64% observed in a chronosequence study, respectively. In contrast, the model systematically underestimated root decomposition of western hemlock at CAH, ponderosa pine, and lodgepole pine at PRF. This is probably because these roots were prone to white-rot, a functional group whose effect was not considered. The presence of resin cores in Sitka spruce, Douglas-fir, and lodgepole pine roots generally reduced decomposition relative to those species without resin cores (e.g., western hemlock and ponderosa pine). For the same species, ROOTDK simulations also indicated that woody roots with resin cores were slower in decomposition than those without resin cores. Simulations indicate that woody root decomposition at CAH and PRF was more sensitive to possible climatic changes than HJA. This is because the current climate conditions are evidently too moist at CAH and too cold and dry at PRF. In contrast, soil temperature and soil moisture regimes at HJA are more optimal for root decomposition, even under a changed climate. Thus, even within the Pacific Northwest region the responses of root decomposition to altered climate can be divergent, with some sites increasing, others decreasing, and others remaining relatively unchanged. Sensitivity analysis of the ROOTDK model indicated that the model is most sensitive to changes in Q_{10} and optimum temperature (Topt) of decomposition. Future research efforts and model improvements are discussed.

6.2 INTRODUCTION

Roots are important structural and functional components of forested ecosystems (Grier et al., 1981; Harris et al., 1977, 1980; Hermann, 1977). A large proportion of forest production is allocated to roots, resulting in a large flux of carbon and nutrients into the belowground system (Cairns et al., 1997; Kurz et al., 1996; Vogt et al., 1986). In coniferous forests, root biomass is an especially large fraction of total stand biomass (Nadelhoffer and Raich, 1992; Vogt et al., 1991). Despite the importance of roots in forest ecosystems, the final fate of this material is not well understood (Berg, 1984; Fahey et al., 1988; Yavitt and Fahey, 1982). This is because most studies of litter dynamics in forest ecosystems have concentrated on aboveground litter (Harmon et al., 1986; Singh and Gutpka, 1977; Swift et al., 1979; Vogt et al., 1986). Far less is known about the dynamics of decomposition, and of carbon and nitrogen of dead woody roots (Heal et al., 1997).

As researchers try to gain a better understanding of the possible impacts of global climate change on carbon and nutrient cycling in forest ecosystems and their feedback to climate, increasing attention is being focused on the belowground system (Walker and Steffen, 1997). Belowground processes represent a significant constraint to forest ecosystem responses to global climate change. Living and dead roots, important components in the belowground system, have been increasingly recognized in soil-mediated responses of forest ecosystems to global climate change (Curtis et al., 1994). The nature and magnitude of these responses are controlled, to a great extent, by the dynamics of root production, growth, and decomposition (Norby, 1994). This is not only because root systems play important roles in carbon and nutrient cycling of forests (Berg, 1984; Waid, 1974) but also because under increasing levels of atmospheric CO_2 more carbon may be allocated to roots due to increasing photosynthesis of plants (Gunderson and Wullschleger, 1994; Norby et al., 1987; Strain, 1987). Elevated atmospheric CO_2 may also lead to a warmer, moister future climate (Houghton et al., 1996) which in turn would generally enhance root decomposition in forest ecosystems. The future carbon store and nutrient balance of forest ecosystems

strongly depends on the degree that increased decomposition of roots is offset by increased production belowground.

Decomposition of roots is influenced by climatic conditions, substrate quality, and the decomposer community (Berg, 1984; Heal et al., 1997; McClaugherty et al., 1984, 1985; Swift et al., 1979). However, the previous studies on root decomposition have primarily focused on the influences of one or two biotic factors, such as root substrate quality (Berg, 1984; Bloomfield et al., 1993; Camire et al., 1991; Fahey et al., 1988; McClaugherty et al., 1984), soil fauna, and soil type (Gijsman et al., 1997; Judas et al., 1995). Few studies have evaluated the integrated effects of biotic (e.g., substrate quality) and abiotic factors (e.g., temperature and moisture) together on root decomposition using a simulation modeling approach. In contrast, a modeling approach has been widely used in the study of aboveground litter decomposition. For example, for the aboveground litter decomposition in the Arctic Tundra alone, at least four simulation models including ABISKO (Bunnel and Dowding, 1974), BARK (Barkley et al., 1978), ARTUS (Miller et al., 1984), GENDEC (Moorhead and Reynolds, 1993) were reported in past two decades. Unfortunately, these aboveground litter decomposition models can not be used directly to simulate woody root decomposition because the decomposition of woody detritus is only grossly similar to fine litter (Harmon and Chen, 1991). For example, woody roots are often attacked by white-rot fungi, which degrade lignin and cellulose (Chapter 2). Thus, the entire conceptual basis for using lignin: nitrogen ratio or lignin-cellulose index as indicators of substrate quality is questionable (Aber et al., 1990; Melillo et al., 1982). Therefore, more specific and process-based decomposition models of woody roots are needed to predict root decomposition and belowground responses to global climatic change.

In this paper we developed a root decomposition simulation model (ROOTDK) to examine the effects of substrate quality, temperature, and moisture on woody root decomposition in Pacific Northwest coniferous forests. The general modeling approach is based on our beliefs that decomposition of roots is controlled by their initial substrate quality and environmental conditions. The initial substrate quality of

woody roots is defined better by separating roots into structural components such as bark, wood, and resin cores than using a substrate index such as lignin:N ratio alone (Chapter 2). An assumption of the ROOTDK model is that the functional roles of the decomposer populations are reflected solely by the effects of temperature and moisture factors. Three questions important to the forests of the Pacific Northwest were addressed in our study:

1. How does structural component of woody roots (e.g., resin cores) influence root decomposition?

2. How do the decomposition rates of woody roots vary with species under current climatic conditions?

3. How will climate changes potentially influence root decomposition at three sites with different thermal-moisture conditions?

6.3 MODEL AND METHODS

6.3.1 Model description

The ROOTDK model includes the effects of substrate quality, temperature, and moisture on root decomposition. The model was implemented using the ECOSIM software developed by Biosystem Analysis Group at Oregon State University.

Effect of substrate quality. Our model is similar to that of Bunnell and Tait (1977):

$$Y_t=M_b\exp^{(-Kb*t)}+M_w\exp^{(-Kw*t)} + M_r\exp^{(-Kr*t)} \quad [1]$$

where Y_t is the mass remaining at time t, M_i is the initial mass of each structural component (i), and K_i is the decay rate of each structural component (i). Unlike the original Bunnell and Tait (1977) model, we separate decaying roots into three structural components: bark, wood, and resin cores. Also the initial mass of each structural component (M_i) changes with the species and size of roots. As in the original model, the decay rate (K_i) is determined by modifying the optimum decay rate (K_{iopt}) by indices of temperature and moisture:

$$K_i= I_{TD}*I_{MD}*K_{iopt} \quad (i= \text{bark, wood, resin cores}) \quad [2]$$

where I_{TD} and I_{MD} are the temperature and moisture decay indices (see below). Each component was assigned an optimum decay rate (K_{iopt}) based on our laboratory incubation study (see Chapter 4). As the proportions of these structural components change with diameter, the overall decay rate also changes.

Our model predicted the changes in substrate quality of roots based on diameter and species. Although the original Bunnell and Tait model divided decomposing material into labile and recalcitrant fractions, it did not predict the decay rates or proportions of these fractions. These parameters had to be solved empirically. We estimated both parameters for structural parts of roots based on size and species. We separated roots into bark, wood, and resin cores, each of which having specific decay rates. The order of decreasing decay rate is wood > bark > resin cores. Resin impregnated cores are found in large roots. The initial mass proportion of root bark (M_{bk}) for a specific species was predicted from root diameter (D):

$$M_{bk} = M_{bk\_min} + M_{bk\_max} EXP^{(-Bbk*D)} \quad [3]$$

where M_{bk_min} is the minimum proportion of the bark, M_{bk_max} is the maximum proportion of the bark, and B_{bk} is the rate at which M_{bk} approaches M_{bk_min} as diameter (D) of roots increases. The initial mass proportion of root wood (M_{wd}) for a specific species was also predicted from root diameter (D):

$$M_{wd} = M_{wd\_max} (1-EXP^{(-Bwd*D)}) \quad [4]$$

where M_{wd_max} is the maximum root wood mass proportion, B_{wd} is the rate at which M_{wd} decreases as the diameter (D) of roots increases. The initial mass proportion of resin cores was calculated based on root bark and wood proportion:

$$M_{re} = 1 - M_{bk} - M_{wd} \quad [5]$$

where M_{re} is the proportion of resin core mass in roots.

We used equations 3, 4, and 5 to predict the changes in the proportions of bark versus wood of Douglas-fir roots (Figure 6-1). This preliminary work indicates that roots are 70% bark at the smallest diameters and approximately 10% bark at the largest diameters.

Effect of soil temperature. In Bunnell and Tait's (1977) model, temperature had only a positive effect on decay or respiration. Our model differs in that if

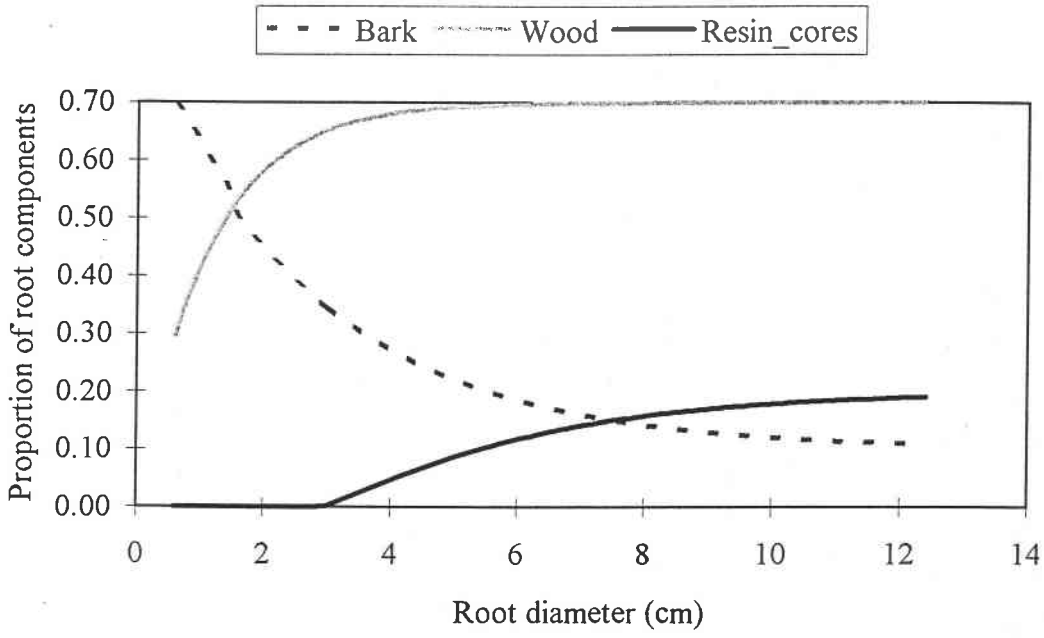

Figure 6-1. Proportion of total mass for bark, wood, and resin cores as a function of root diameter for Douglas-fir roots.

temperature exceeds the optimum temperature then root decomposition decreases (Figure 6-2). We used this negative effect function to better handle situations where increased radiation can heat soils above the lethal limits for decomposers (e.g., recent clear-cuts). When temperature is below the optimum, the effect of temperature is:

$$TI=Q_{10}^{[(T-10)/10]} \quad [6]$$

where TI is the increase or decrease from a standard of 10^0C, and Q_{10} is the rate of increase for a 10^0C change in temperature (T). Q_{10} was set to 3-4 based on the annual temperature (5-10 ^{0}C) of three sites used in this study (Chapter 4). As TI has a range exceeding 1, we rescaled this variable by dividing it by the value of TI when temperature is optimal (T_{opt}):

$$TI_{max}= Q_{10}^{[(Topt-10)/10]} \quad [7]$$

where TI_{max} is the maximum value of TI.

The effect of lethal temperature (TL) is determined by a function that has a value of 1 until that limit is reached and then declines to 0 when the temperature limit is exceeded:

$$TL=Exp[-(T/(T_{opt}+4))^{25}] \quad [8]$$

The optimum temperature was set at 30 or 40^0C depending on the species of roots (see Chapter 4). The combined effects of temperature result in an index (I_{TD}) that ranges from 0 to 1:

$$I_{TD}=(TI^* TL)/TI_{max} \quad [9]$$

Effect of moisture. As in the original model, moisture controls in decomposition are included two ways. The first is through matric potential which makes water unavailable for decomposers. Unlike the original model, however, we assume decomposition ceases when moisture content drops below the fiber saturation point (25-30%). The second effect of moisture is to limit oxygen diffusion when moisture content is too high (Killham, 1994). We modeled each effect separately. The equation for matric potential is:

$$ML=(1-exp[-(M/M_{min}+20)])^5 \quad [10]$$

where ML is the matric limitation, which ranges in value from 0 to 1, M is the moisture

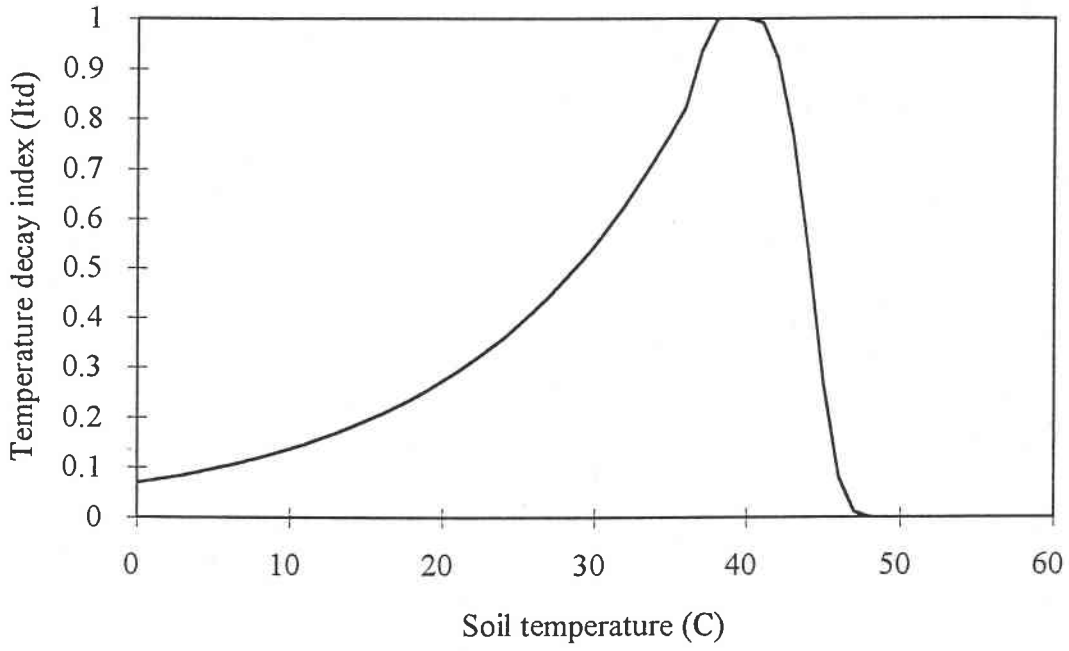

Figure 6-2. Relationship of temperature decay index (Itd) to soil temperature.

content of the roots, and M_{min} is the fiber saturation point. When M is > M_{min} the matric limit function increases to 1.

Excessive moisture can retard decomposition by reducing the rate oxygen diffuses. We assume that above given moisture content this process becomes limiting to decomposition. The function describing this response is:

$$DL=\exp[-(M/M_{max} - 20)^{20}] \quad [11]$$

where DL is the diffusion limitation which ranges in value from 0 to 1, M is the moisture content of the roots, and M_{max} is the moisture content when diffusion limitation suppresses decay. This function remains at 1 until the maximum moisture content that suppresses decay (M_{max}) is reached. When M > M_{max} the function decreases to 0. The overall effect of moisture content on decay (I_{MD}) is calculated by multiplying the matric and diffusion limitations (Figure 6-3).

$$Imd = ML * DL \quad [12]$$

6.3.2 Methods and parameterization

Data from field root decomposition and laboratory incubation studies were used to parameterize and validate the ROOTDK model (Figure 6-4). Field sites included Cascade Head Experimental Forests (CAH), H. J. Andrews Experimental Forests (HJA), and Pringle Falls Experimental Forests (PRF). For detailed descriptions of these sites refer to Chapter 2. Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), and lodgepole pine (*Pinus contorta*) were used in this study. The mass proportions of different structural components in woody roots were calculated based on the measurements of fresh roots prior to the establishment of a long-term root decomposition time series study (see Chapter 3). Laboratory incubation results of decomposing roots were used to parameterize the optimum decay rate-constant of roots and the effects of temperature and moisture on root decomposition in the model. The ROOTDK model was validated by the results of chronosequence studies of root decomposition.

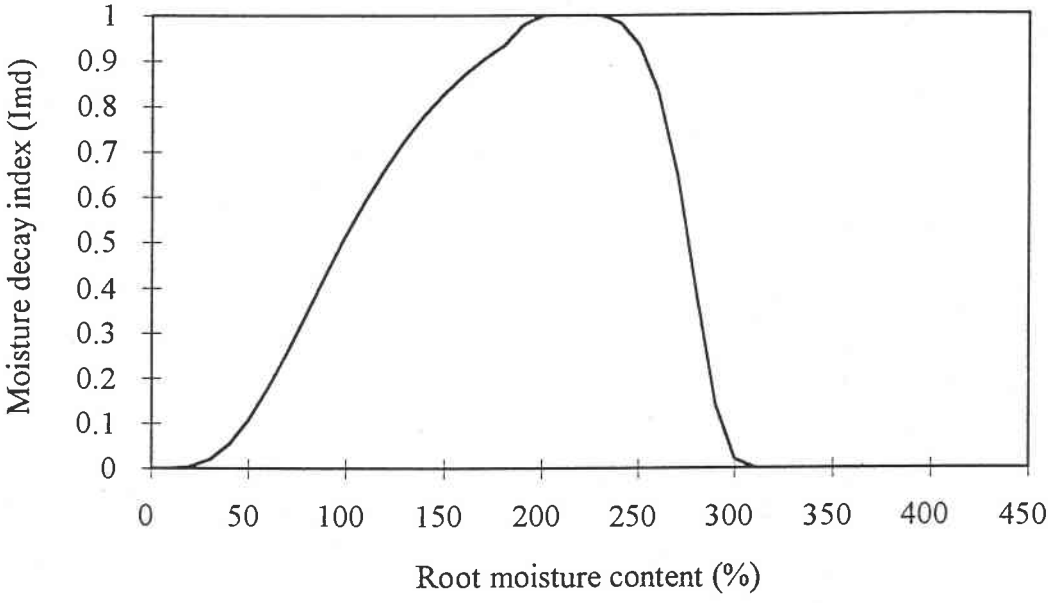

Figure 6-3. Moisture decay index (Imd) as a function of root moisture content.

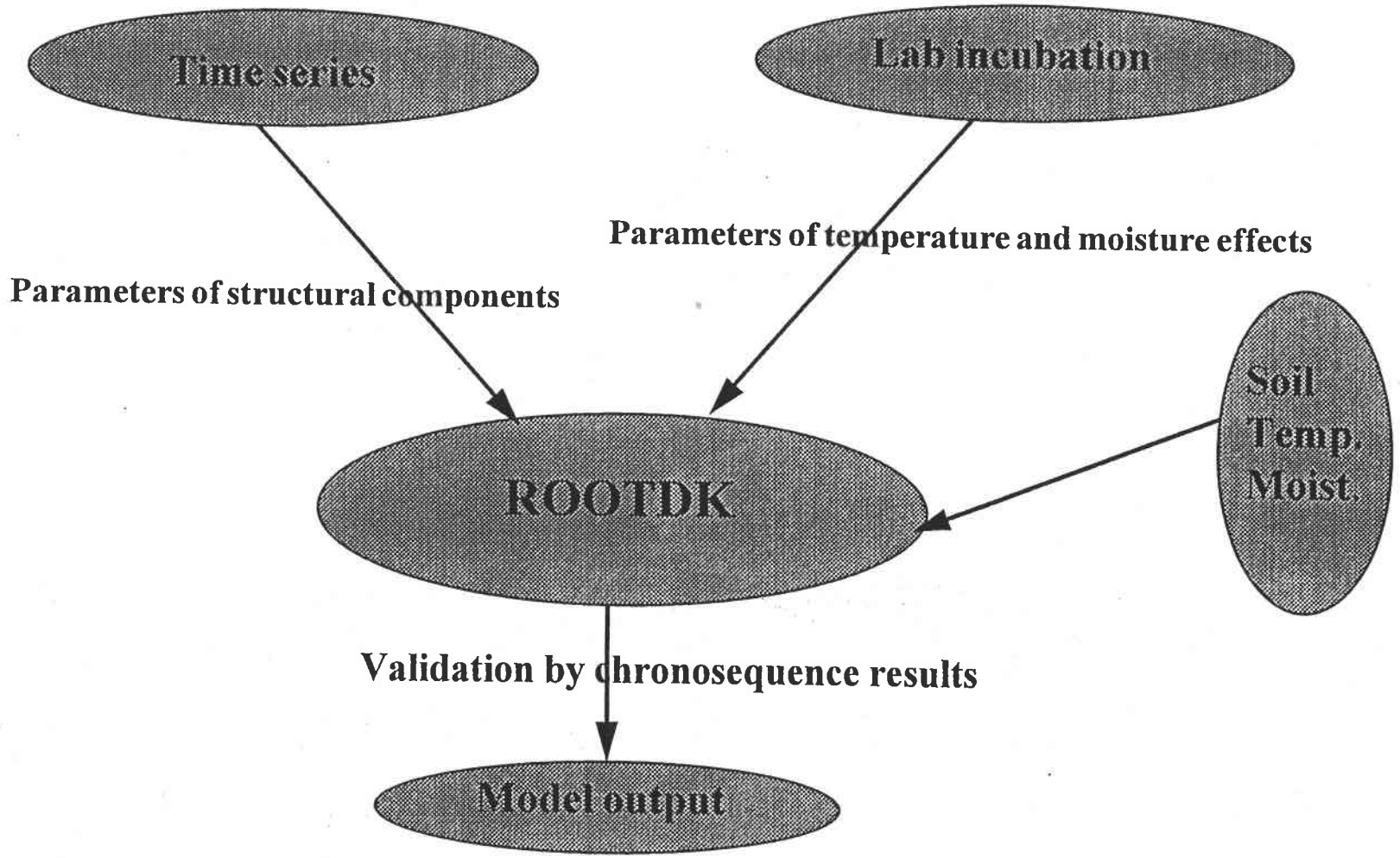

Figure 6-4. ROOTDK model

Driving variables included root diameter, which was used to calculate the proportion of structural component, soil temperature, and root moisture (Table 6-1). Soil microclimate data were collected at each site from September 1995 to September 1997. We measured the soil temperature at 20, 40, and 60 cm depths and air temperature (1 m from ground level) using thermisters (Yellow Springs, YSI 44006). Air and soil temperatures were recorded hourly and every 12 hours, respectively. Time Domain Reflectometry (TDR) (Fritschen and Gay, 1979) was used to measure the volumetric soil moisture of the same three soil depths at each plot once every three months. The relationship between soil moisture and root moisture was modeled as a diffusion process with roots wetting faster than they dried (Chapter 5). Seasonally averaged soil temperature and root moisture data (of the 20-cm depth sample) were used as the abiotic variables to drive the model.

We simulated 30 years of decomposition of the five species of woody roots (3 cm in diameter) under current soil temperature and moisture conditions. We also tested the impacts of four climate change scenarios on decomposition of Douglas-fir roots at the three sites. The four climate change scenarios consisted of increased temperature but unchanged moisture (ITUM), increased temperature and decreased moisture (ITDM), unchanged temperature and increased moisture (UTIM), and both increased temperature and moisture (ITIM). In these simulations, soil temperature was increased 3 ^{0}C more than current seasonal temperatures and soil moisture was changed by 10% from current seasonal averages of soil gravemetric moisture, which is equivalent to a 25, 24, and 21% change in decomposing root moisture at CAH, HJA, and PRF, respectively (see Chapter 3 and Chapter 5). The time step for these simulations was 3 months.

We performed sensitivity analysis of the ROOTDK model by separately increasing and decreasing the value of each parameter by 10%. Mass loss of woody roots was the response state variable. Ten parameters including Q_{10} and Topt were evaluated. This analysis was carried out by simulating Douglas-fir root decomposition under the current HJA climatic condition.

Table 6-1 Parameters, driving, and state variables of the ROOTDK model. Equations are presented under methods.

(a) List of model parameters

Parameters	Equation #	Value	Units	Definition
I_{MD}	2,12	0 - 1	unitless	Moisture decay index
I_{TD}	2, 9	0 - 1	unitless	Temperature decay index
K_i	1, 2	varied	/year	Actual decay rate of structural component i of roots
K_{iop}	2	varied	/year	Optimum decay rate of structural component i of roots
M_{bk_min}	3	0.1	unitless	Minimum proportion of bark component
M_{bk_max}	3	0.45	unitless	Maximum proportion of bark component
M_{wd_max}	4	0-1	unitless	Maximum wood proportion of woody roots
M_{min}	10	30	%	Minimum moisture content for root decay
M_{max}	11	300	%	Maximum moisture content for root decay
Q_{10}	6	3--4	unitless	Rate of increase for a 10^0 C increase of temperature
T_{opt}	7, 8	30-40	^{0} C	Optimum temperature for root decomposition

(b) List of driving variables and state variables

Variables	Equation #	Value	Units	Definition
Driving variables				
D	3	> 2	mm	Root diameter
T	4, 6	varied	^{0} C	Soil seasonally mean temperature at 20 cm depth
M	8, 9	varied	%	Seasonally mean root moisture content at 20 cm depth
t	1	varied	Mon./yr.	Time
State variables				
Yt	1	0 - 1	Unitless	Root mass remaining fraction at time t

6.4 RESULTS

6.4.1 Sensitivity analysis

Among the 8 parameters examined, Q_{10} and Topt (optimum temperature for decomposition) were the two most influential parameters (Figure 6-5). A ten percent increase or decrease of Q_{10} and Topt resulted in 9% and 7% increase or decrease of mass loss. The impact of the rest of the parameters were minimal, ranging from 1-4% change of mass loss given a 10% change in parameter values.

6.4.2 Simulation under current climate conditions

6.4.2.1 Root decomposition of five species

Predicted and observed decomposition patterns were comparable for Sitka spruce, Douglas-fir, and western hemlock at the HJA site. Decomposition was underpredicted, however, for lodgepole pine, ponderosa pine at PRF and western hemlock at CAH (Figure 6-6). For the three species predicted well by the ROOTDK model, observed and predicted results differed by less than 10%, except for the Sitka spruce roots at CAH after 7 years of decomposition. After 30 years of decomposition, the ROOTDK model predicted that Sitka spruce, Douglas-fir, and western hemlock (at HJA) lost 51, 42, 61% of the initial mass in comparison to observed percentages of 50, 32, and 64%, respectively, at CAH and HJA. However, the model underestimated the mass loss for both pine species at PRF and western hemlock at CAH (Figure 6-6). Model predictions for lodgepole pine and western hemlock at CAH were 20% lower than what was observed after 7 years. Moreover, for ponderosa pine, the difference between predicted and observed values increased from 30% at 7 years to more than 60% at 25 years.

6.4.2.2 Effects of resin cores

The presence of resin cores in woody roots reduced root decomposition in comparison to woody roots without resin cores (Figure 6-7). On average, Douglas-fir,

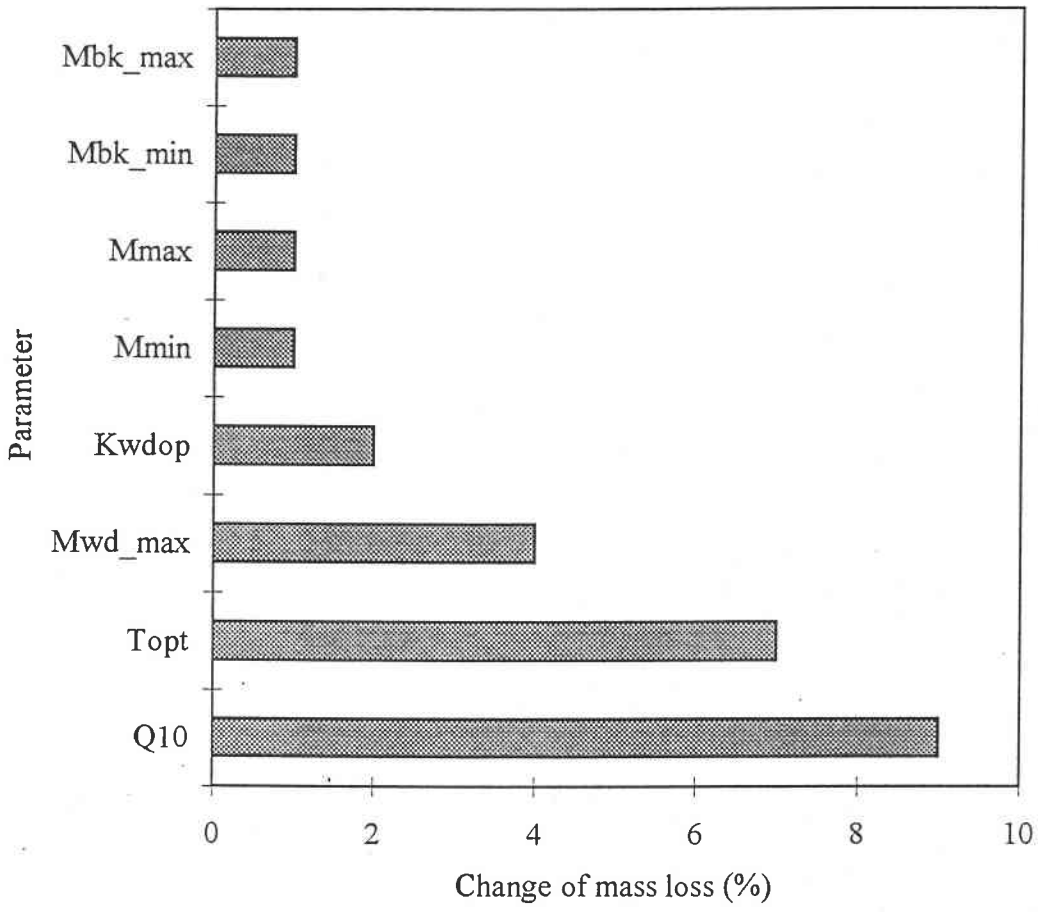

Figure 6-5. Sensitivity analysis of a 10% change in parameter values--effects on root mass loss (see Table 6-1 for parameter definitions).

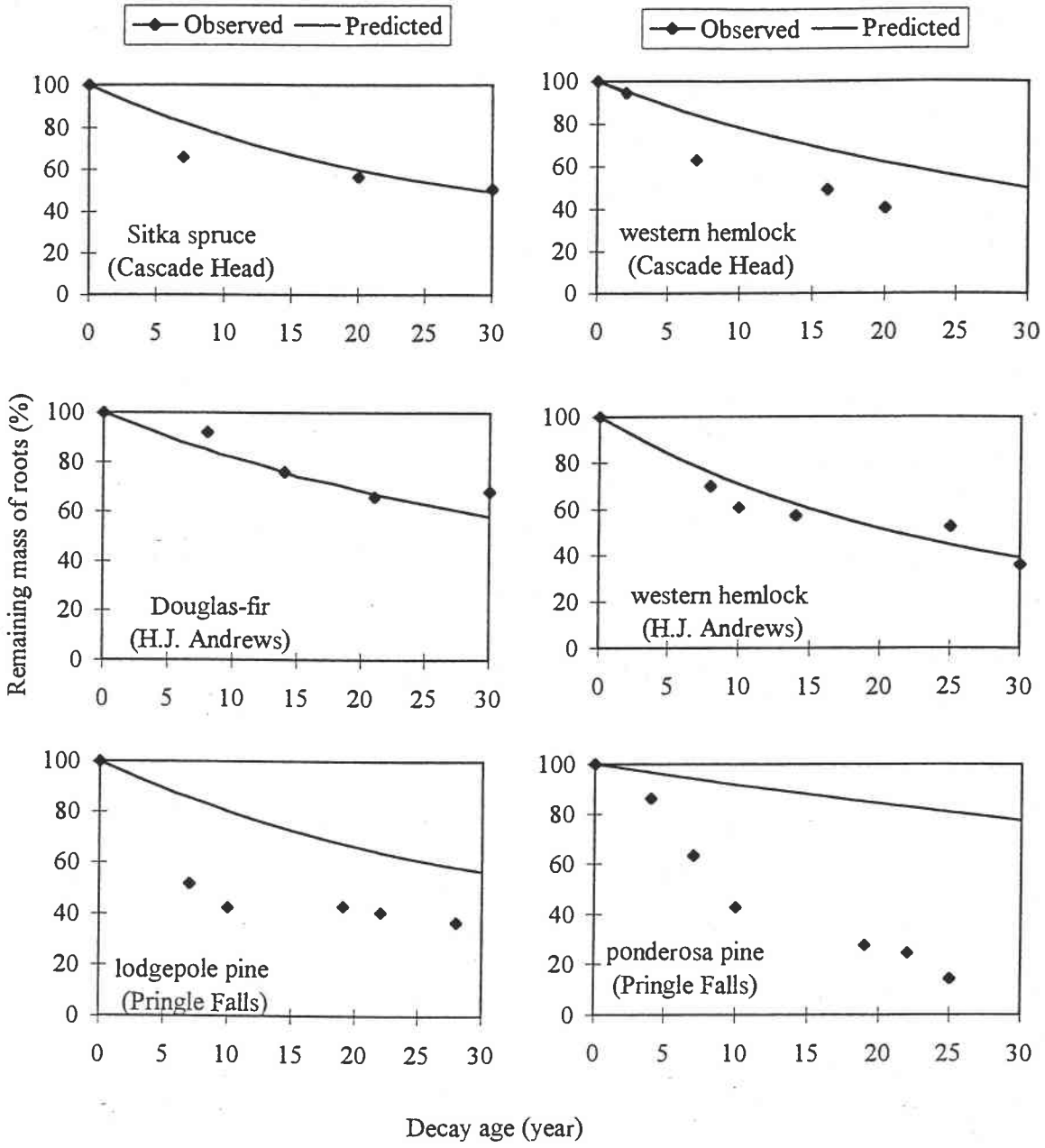

Figure 6-6. Predicted and observed decomposition of five species of woody roots at three sites.

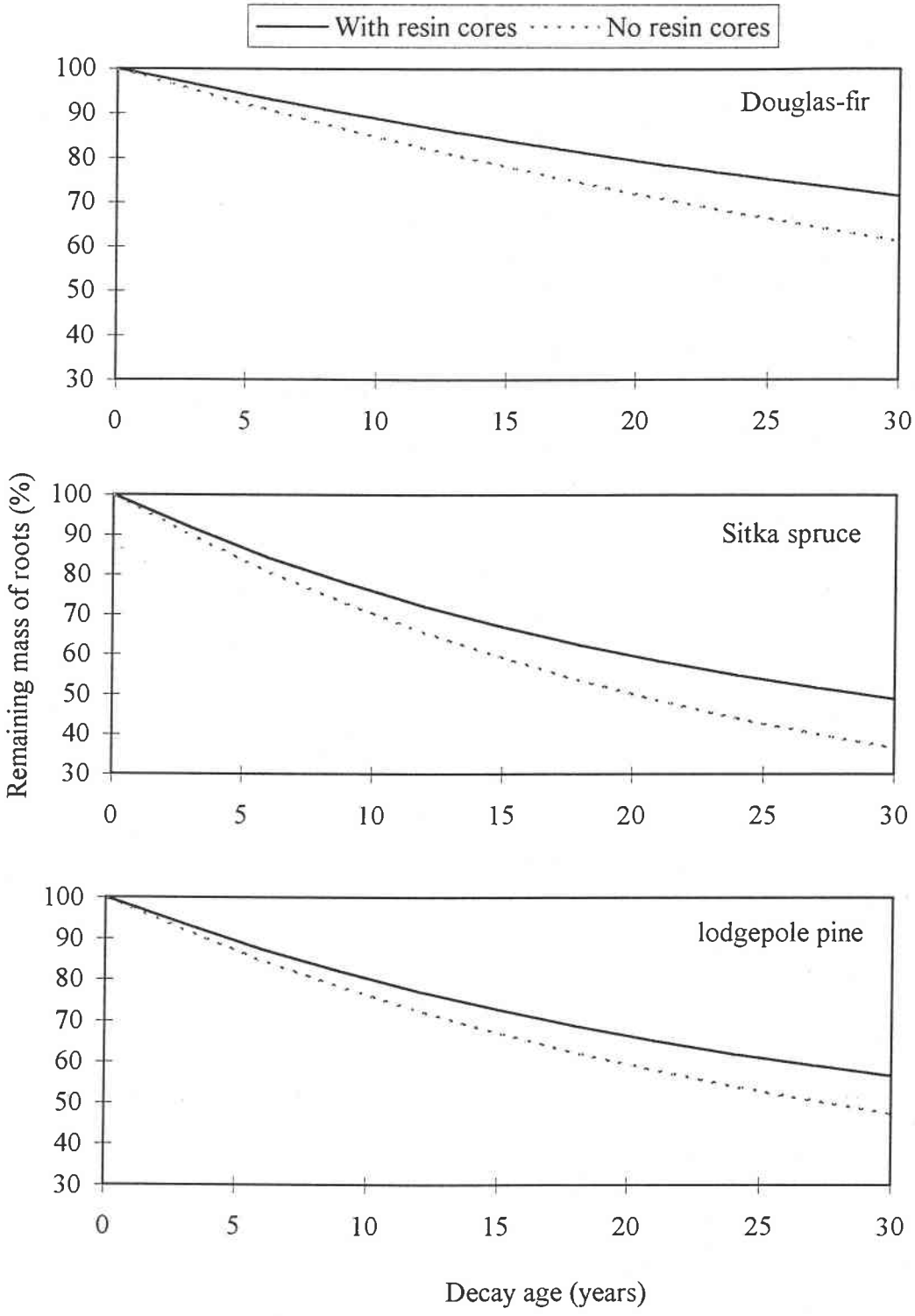

Figure 6-7. Simulated decomposition of woody roots with and without resin cores.

Sitka spruce, and lodgepole pine woody roots with 20% resin cores lost 10% less mass over 30 years of decomposition than those that lacked resin cores. This pattern is qualitatively similar to the chronosequence study (Chapter 2).

6.4.3 Simulation of four climate change scenarios

For the increasing temperature and unchanged moisture (ITUM) scenario, root decomposition at all three sites increased in comparison to current temperature and moisture conditions (Figure 6-8). In decreasing order the sites were HJA > CAH > PRF, the same order as for current climate simulation. After 30-years of decomposition in a warmer climate, Douglas-fir roots were predicted to lose 5, 5, and 3% more mass compared to mass loss under the current climate at CAH, HJA, and PRF, respectively.

The responses of root decomposition at the three sites differed in the increasing temperature and decreasing moisture (ITDM) scenario (Figure 6-9). Root decomposition at CAH increased whereas at PRF it decreased. For example, decomposing roots were predicted to lose 20% more mass after 30 years at CAH. In contrast, after the same period the remaining root mass at PRF would be 10% less. Root decomposition at HJA was not altered compared to the current climate simulation. Therefore, root decomposition was CAH > HJA > PRF under a warmer and drier climate.

For the unchanged temperature and increasing moisture (UTIM) scenario, three patterns of changes were observed (Figure 6-10). Root decomposition at CAH site decreased, with 24% less mass loss in 30 years than under the current climate. In contrast, about 10% more root mass was lost at PRF for the same period in a wetter climate. Root decomposition at HJA increased slightly, with 2% more mass loss in comparison to the current climate. The site order for root decomposition was HJA > PRF > CAH.

The responses of three sites to increasing both temperature and moisture (ITIM) scenario were similar to the UTIM scenario (Figure 6-11). CAH became the site with the slowest decomposition, PRF the next, and HJA the fastest one. However,

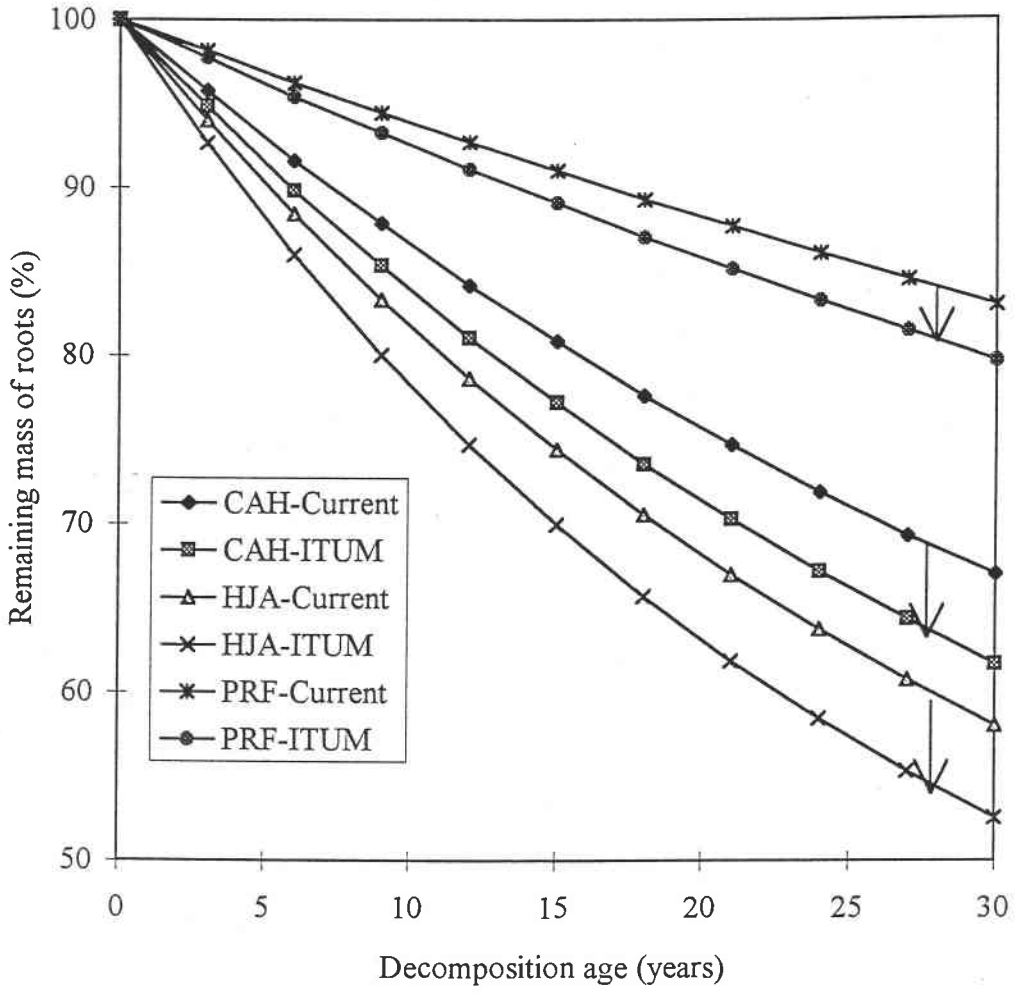

Figure 6-8. Comparison of root decomposition under current and ITUM climate scenarios. Arrow indicate the change from current climate*.

* ITUM: increased soil temperature and unchanged soil moisture.
CAH, HJA, and PRF refer to Cascade Head, H.J. Andrews, and Pringle Falls sites.

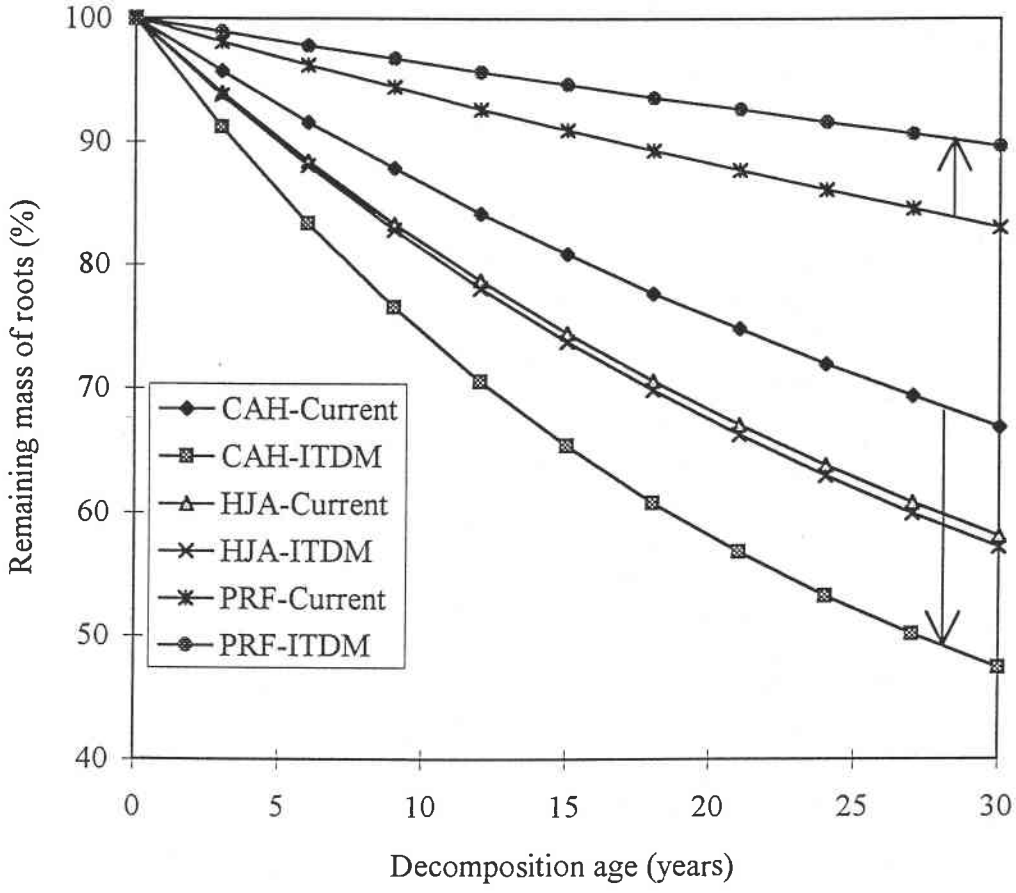

Figure 6-9. Comparison of root decomposition under current and ITDM climate scenarios. Arrow indicate the change from current climate*.

* ITDM: increased soil temperature and decreased soil moisture.
CAH, HJA, and PRF refer to Cascade Head, H.J. Andrews, and Pringle Falls sites.

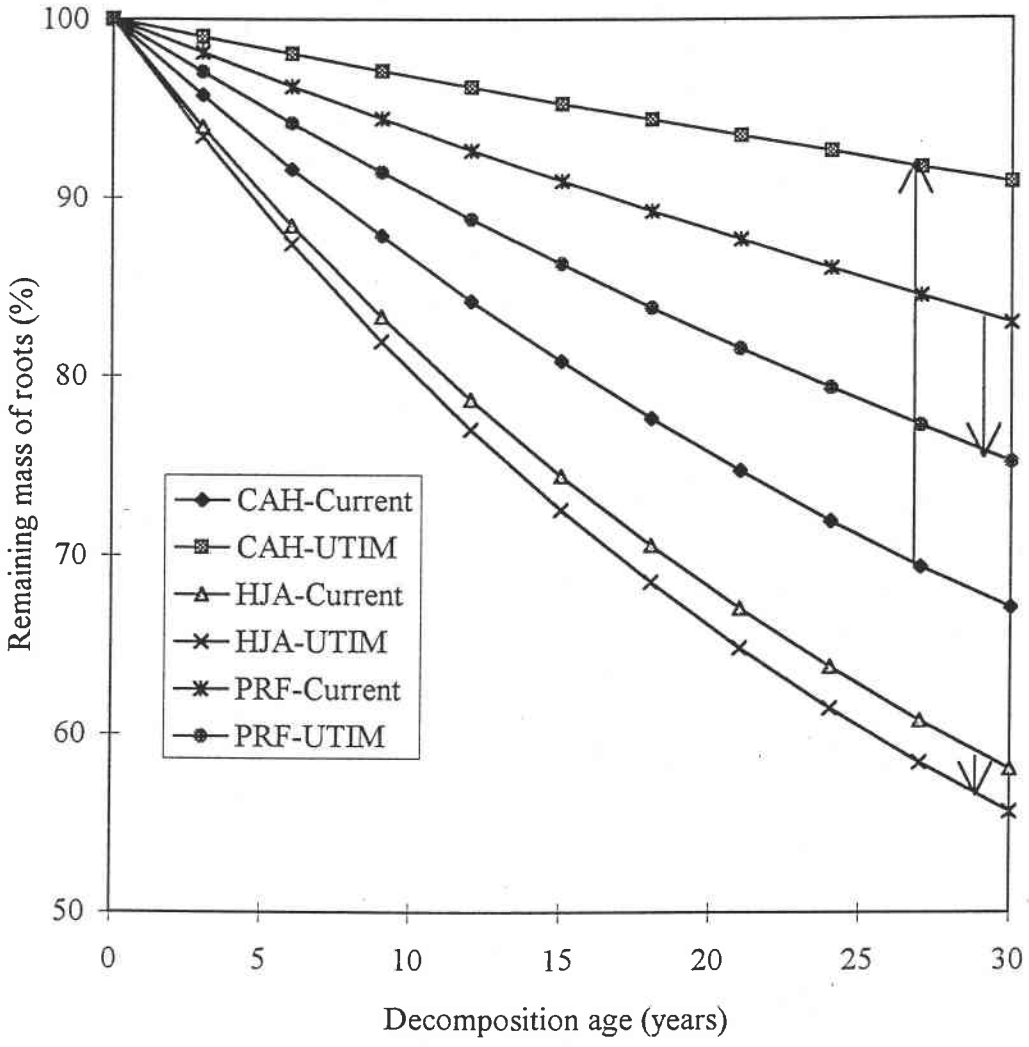

Figure 6-10. Comparison of root decomposition under current and UTIM climate scenarios. Arrow indicate the change from current climate*.

* UTIM: unchanged soil temperature and increased soil moisture.
CAH, HJA, and PRF refer to Cascade Head, H.J. Andrews, and Pringle Falls sites.

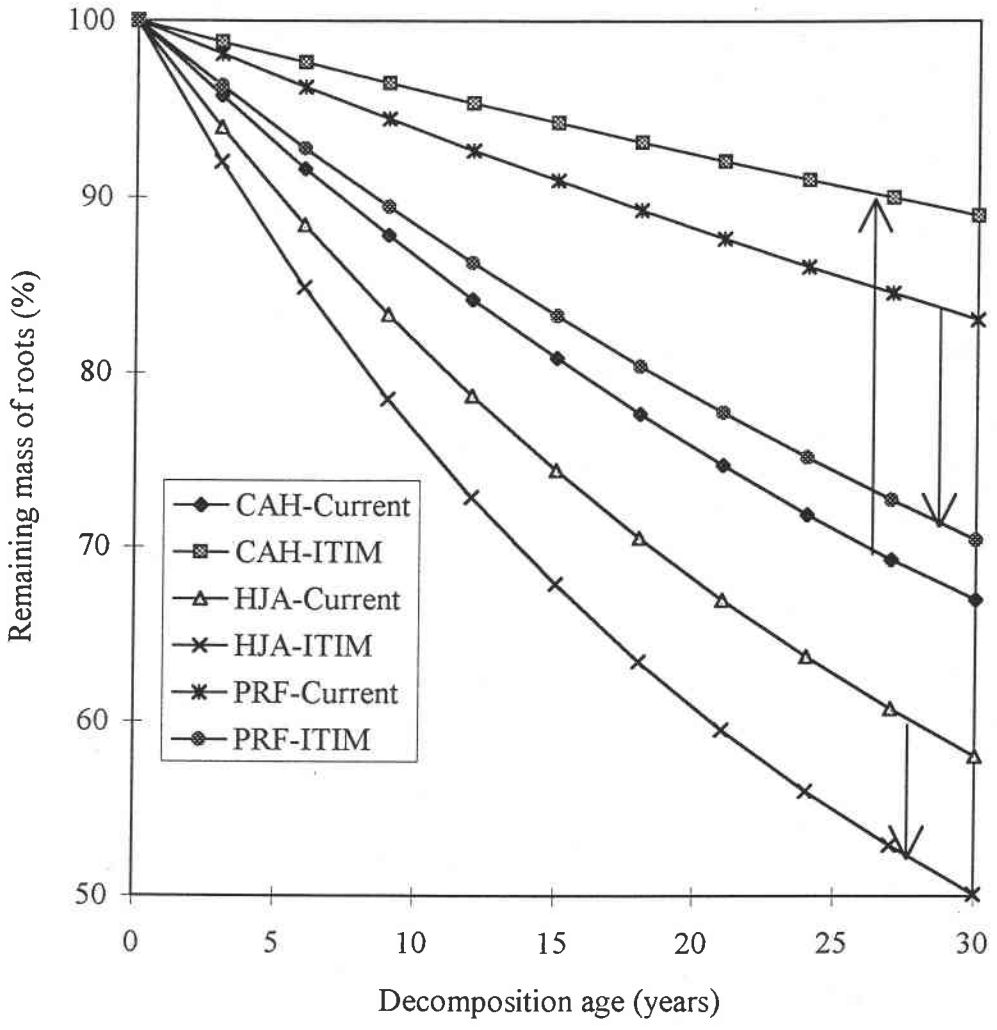

Figure 6-11. Comparison of root decomposition under current and ITIM climate scenarios. Arrow indicate the change from current climate*.

* ITIM: increased both soil temperature and soil moisture.
CAH, HJA, and PRF refer to Cascade Head, H.J. Andrews, and Pringle Falls sites.

root decomposition at HJA and PRF sites indicated < 10% more mass loss than the UTIM scenario due to combined effects of warming and wetting climate.

6.5 DISCUSSION

6.5.1 Model performance evaluation and analysis

Our ROOTDK model appeared to reasonably mimic the observed decomposition trends of Sitka spruce, Douglas-fir, and western hemlock (HJA) in the western Cascades of Oregon. This suggests that a simple mechanistic-based model can be useful in simulating the belowground root decomposition process. However, the systematic underestimation of decomposition for lodgepole pine, ponderosa pine in the drier eastern foothills of the Cascades, and western hemlock at a wet coastal site indicates the model may not capture all the factors controlling decomposition. In the ROOTDK model, a critical assumption is that the functional roles of decomposers are reflected by temperature and moisture decay indices. This might not be always true. We found root species varied in rot type (Chapter 2). For example, the woody roots of ponderosa pine and lodgepole pine were prone to white-rot whereas Sitka spruce and Douglas-fir were prone to brown-rot. For western hemlock, white- and brown-rot both occurred (Chapter 2). White-rot degrade lignin as well as cellulose. In contrast, brown-rot degrade cellulose but not lignin (Kirk and Farrell, 1987). This study indicates that the ROOTDK model predicted the decomposition of roots prone to brown-rot such as Sitka spruce and Douglas-fir much better than those prone to white-rot (Figure 6-6). However, it is not clear why the model performance was better in predicting root decomposition of western hemlock at HJA than at CAH, although the frequency of occurrence of brown-rot in decomposing roots was similar (42% versus 44% at both sites) (Chapter 2).

6.5.2 Effects of substrate quality--resin cores

Substrate quality of woody roots is a dominant factor controlling root decomposition (Berg, 1984; Heal et al., 1997; McClaugherty et al., 1984, 1985). Resin

cores analogous to branch knots are common in the coarse woody roots of many coniferous trees (Chapter 2). They are the most recalcitrant component of woody roots. Therefore the presence of resin cores in Sitka spruce, Douglas-fir, and lodgepole pine roots generally reduced the decomposition relative to those species without resin cores (e.g., western hemlock and ponderosa pine) (Figure 6-6). To a great degree, the species differences in decomposition rates of woody roots are due to this structural component--resin cores. Moreover, intraspecific decomposition comparison based on the ROOTDK model simulations also indicated that the woody roots with resin cores were slower in decomposition than those without resin cores (Figure 6-7). The difference of mass loss can be more than 10% after 30-years of decomposition (Figure 6-7).

6.5.3 Impacts of climate change on root decomposition

The degree that global climatic change will influence the decomposition of roots of CAH, HJA, and PRF depends on not only the potential magnitude of temperature and precipitation change in the Pacific Northwest region, but also on the current site-specific environment conditions. The dominant environmental limiting factors appear to have varied with site. For PRF site, low soil temperature in winter and spring (Figure 6-12) and low root moisture content in summer and fall (Figure 6-13) appear to have limited the microbial processes and in turn slowed down root decomposition. Soil temperature at PRF could reach as low as 1^0 C in winter and early spring (Figure 6-12) and this cold period lasted several months which would have retarded the activity of decomposers (Chen and Harmon, unpublished data). Also, dead root moisture at PRF was generally low, especially in comparison to the other two sites (Figure 6-13). Although CAH showed the most favorable thermal conditions among the three sites ranging from 7 to 14^0 C during the year, the moisture content of decomposing roots was very high at this site ranging from 300 to 500% (Figure 6-13). This high moisture content may have reduced oxygen diffusion in the belowground system (Killham, 1994), resulting in anaerobic conditions that would hinder decomposition. Among the three

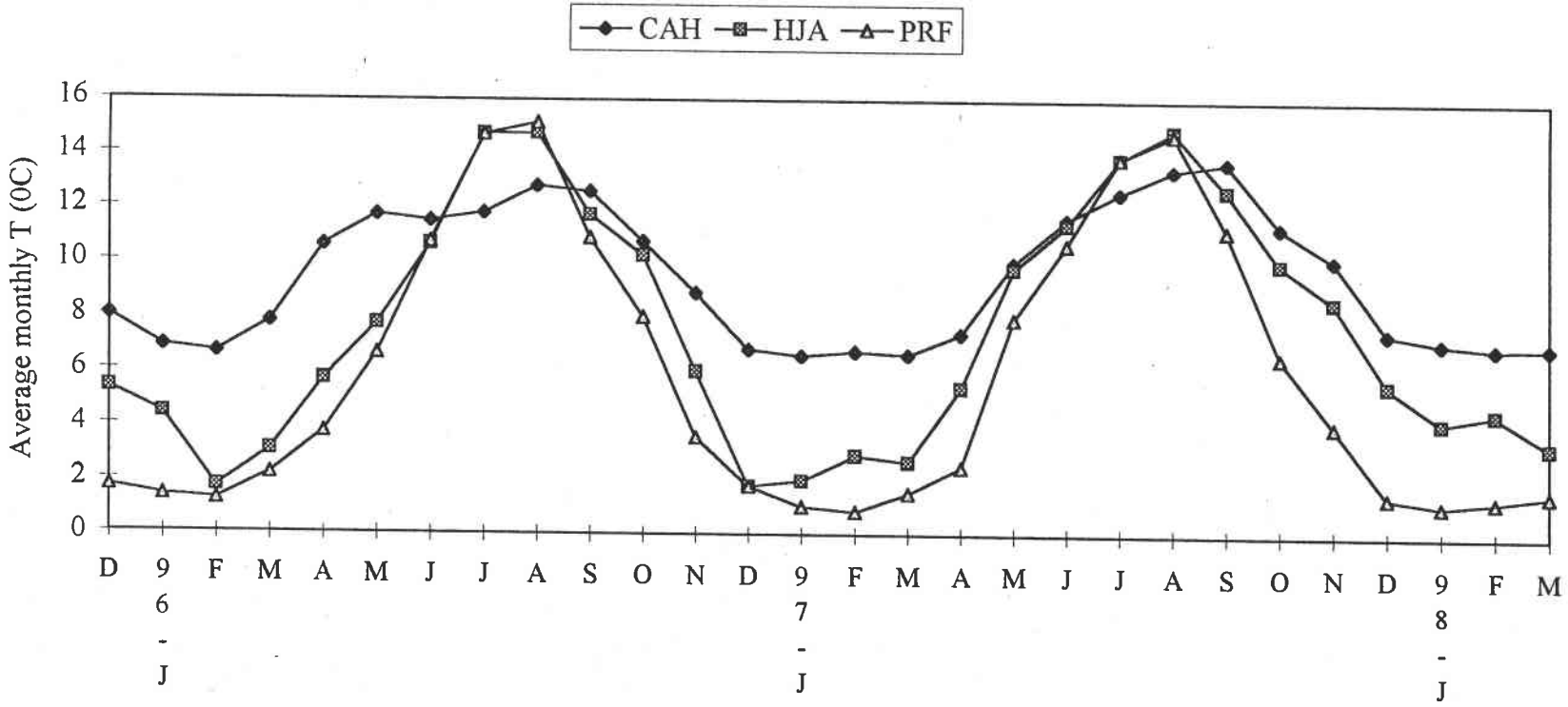

Figure 6-12. Seasonal patterns of soil temperature (20 cm) of three sites*.

*: each point was the mean temperature of 3-4 plots
CAH, HJA, and PRF refer to Cascade Head, H.J. Andrews, and Pringle Falls sites.

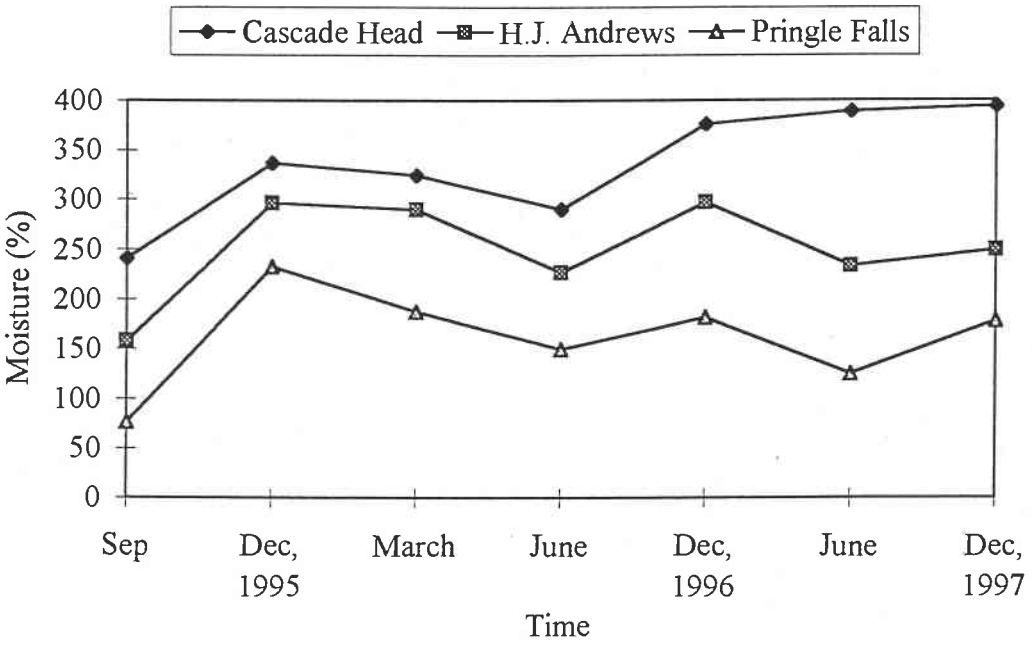

Figure 6-13. Moisture dynamics of fine roots at three sites.

sites, the current thermal-moisture conditions at HJA are best for root decomposition (Figure 6-12 and Figure 6-13). Although the lowest soil temperature for HJA was around 2^0 C in December (Figure 6-12), it persisted for a much shorter period than at PRF. More importantly, root moisture content at HJA was between 150% to 300%, an optimum range for decomposition (see Chapter 4). Among the three sites, the favorability of current climate conditions for root decomposition is HJA > CAH > PRF. This was further confirmed by the decomposition simulation of Douglas-fir roots under current climate conditions by the ROOTDK model, showing decomposition was fastest at HJA site, second at CAH, and the slowest at PRF (Figure 6-8).

The impacts of 4 climate change scenarios on woody root decomposition varied with site (Figure 6-14). The ITUM scenario enhanced root decomposition slightly among all three sites (Figure 6-8). However, the other three scenarios had more profound impacts on root decomposition. For ITDM scenario, three patterns of root decomposition responses occurred among the three sites. Root decomposition increased at CAH due to the mitigation of excess moisture, was unchanged at HJA, and slowed down at PRF due to the same drying effect (Figure 6-9). In both the UTIM and ITIM scenarios, root decomposition was slower at CAH due to the limiting effects of excess moisture, but higher at PRF where more moisture became available for decomposers. These two climate change scenarios also slightly increased root decomposition of HJA (Figure 6-10 and Figure 6-11). Therefore, the responses of root decomposition of the three sites to changed climate clearly indicated that root decomposition at CAH and PRF was more sensitive to climate change than HJA (Figure 6-14). This is because the current thermal-moisture conditions are limiting root decomposition at CAH and PRF sites. A change of any these limiting climate conditions would enhance or hinder root decomposition. In contrast, soil temperature and moisture regimes at HJA are more optimal for root decomposition, even under the changed climates.

After comparing the net effects of climate change scenario ITUM and UTIM on root decomposition at the three sites, we found a 10% soil moisture change had larger impacts on root decomposition in the Pacific Northwest than a 3 ^{0}C soil temperature

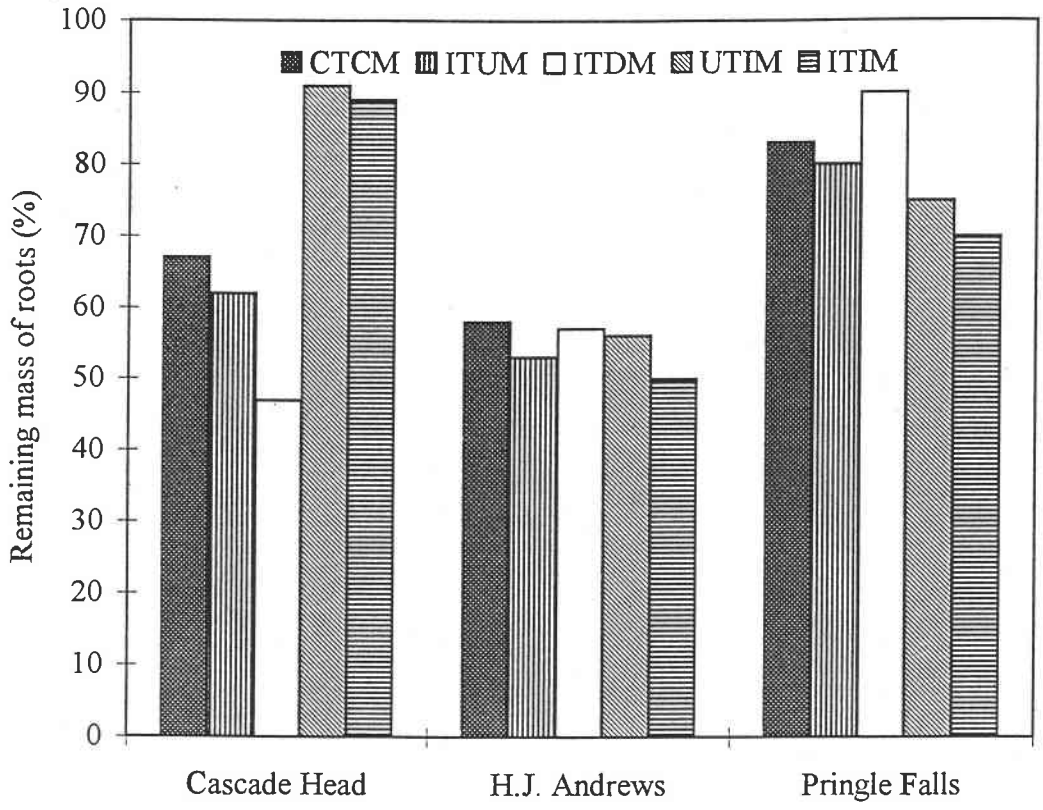

Figure 6-14. Climatic change impacts on mass loss of woody roots after 30 years of decomposition at the three sites.

CTCM: current soil temperature and moisture condition.

ITUM: increased soil temperature 3 ^{0}C and unchanged soil moisture.

ITDM: increased soil temperature 3 ^{0}C and decreased soil moisture 10%.

UTIM: unchanged soil temperature and increased soil moisture 10%.

ITIM: increased both soil temperature 3 ^{0}C and soil moisture 10%.

change, although both scenarios had little impact on root decomposition at HJA site (Figure 6-14). This suggests that root decomposition at CAH and PRF site may be more sensitive to precipitation than temperature change in the future.

Even within the Pacific Northwest region the responses of root decomposition to altered climate can be divergent, with some sites increasing, others decreasing, and others remaining relatively unchanged. Understanding these site-level patterns of root decomposition under changing climate will be important in the analysis of global climate change impacts on belowground system in the Pacific Northwest. The site-level patterns of responses of root decomposition to climate changes are determined by the current site-specific climate conditions and the degree of future climate change.

6.5.4 Future research efforts and model improvements

Sensitivity analysis indicated that Q_{10} and the optimal temperature (Topt) for root decomposition are the most two influential parameters in the model. Therefore it is important to parameterize these two parameters correctly to improve the model performance. Controls on Q_{10} and Topt were understood in coniferous forests in the Pacific Northwest (Chapter 4). However, it is not clear that how these two parameters will vary with different biomes. Further understanding of the controls of climate and soil decomposers on these two parameters in root decomposition should increase the application of the ROOTDK model to other regions.

Two important aspects are proposed to improve this model. First, we suggest to further separate root wood into two components: lignin and cellulose/hemicellulose. Woody roots are composed of almost one-third lignin and two-thirds cellulose/hemicellulose (see Chapter 3). Moreover, lignin can be decomposed only by white-rot and cellulose/hemicellulose can be decomposed by brown- and white-rot. Second, we propose to incorporate the controls on white- and brown-rot functional groups into to the model. The new model is expected to perform better in predicting the decomposition of woody roots dominated by white-rot than the current version of ROOTDK.

6.6 CONCLUSIONS

The ROOTDK model can be used to evaluate the effects of species, temperature, and moisture on root decomposition in the Pacific Northwest. The model predicted decomposition of Sitka spruce, Douglas-fir, and western hemlock at HJA well, but underestimated root decomposition of lodgepole pine and ponderosa pine at PRF, and western hemlock at CAH under current climatic conditions. For the same species, the woody roots with resin cores decomposed more slowly than those without resin cores. Woody root decomposition at CAH and PRF was more sensitive to climatic changes than HJA. This is because the current climate conditions are evidently too moist at CAH and too cold and dry at PRF. In contrast, soil temperature and soil moisture regimes at HJA was more optimal for root decomposition. This indicates that even within the Pacific Northwest region the responses of root decomposition to altered climate can be divergent, with some sites increasing, others decreasing, and others remaining relatively unchanged. Sensitivity analysis of the ROOTDK model indicated that Q_{10} and the optimum temperature (Topt) of decomposition are the two most influential parameters in the model. Understanding the factors controlling white- and brown rot and improving the model performance for species prone to white-rot will be key future research efforts.

6.7 ACKNOWLEDGMENTS

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7. SUMMARY

1. A chronosequence study indicated that a structural component-oriented approach of woody root decomposition provided a better estimation of long-term mass loss than initial substrate quality indices. The occurrence of resin cores in woody roots of Douglas-fir, Sitka spruce, and lodgepole pine greatly slowed decomposition of these species. The effect of climate on root decomposition was apparently overridden by differences in species.

2. During the first two years of decomposition in a time series study, species significantly controlled mass loss in fine, small roots, but not in medium, large, and jumbo sized roots. For the same time period, site differences had little impact on the decomposition of woody roots, regardless of root size. Woody root decomposition decreased with increasing root size.

3. Both field decomposition studies indicated that initial substrate indices were not good predictors of decomposition rate-constants (k) of roots larger than 1 cm in diameter. However, lignin:N ratio and phenols:N ratio were good predictors of k for fine and small roots (< 1 cm), respectively.

4. In both the chronosequence and decomposition time series experiment, dead woody roots started to release nitrogen in the early stages of decomposition. Therefore they could be an important nitrogen source in forest ecosystems after large-scale disturbances such as clear-cutting or forest fire.

5. Laboratory incubations showed that dead root respiration increased with temperature and reached the maximum at 30-40 °C, then decreased. The Q_{10} of root respiration was influenced significantly ($P < 0.01$) by incubation temperature range, but not by species, or decay class. Dead root respiration increased with root moisture,

reached an optimum range when moisture was between 100 and 275%, and then decreased above that point.

6. The direction of temperature and moisture change did not significantly influence root respiration, indicating hysteresis did not occur for the temperature and moisture ranges examined.

7. Exchange of moisture between dead roots and soils appeared to follow a diffusion process. A simple diffusion model performed well in simulating observed moisture dynamics of dead roots in soils. Experiments and the model indicated that moisture of larger roots equilibrated more slowly than that of small roots. Dead roots gained moisture faster than they lost it in soils.

8. The ROOTDK model, which synthesized the controls of substrate quality, temperature, and moisture on root decomposition, captured the overall mass loss pattern of Sitka spruce, Douglas-fir, and western hemlock at HJA in the first 30 years. However, the model underestimated root decomposition of western hemlock at CAH, as well as ponderosa pine, and lodgepole pine at PRF. This is probably because these species were prone to white-rot, a functional group whose effect was not considered in the model.

9. Woody root decomposition at CAH and PRF was more sensitive to possible climatic changes than HJA because the current conditions are evidently too moist at CAH and too cold and dry at PRF. In contrast, current soil temperature and soil moisture regimes at HJA were more optimal for root decomposition. Thus, even within the Pacific Northwest region the response of root decomposition to altered climate can be divergent, with some sites increasing, others decreasing, and others remaining relatively unchanged.

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