AN ABSTRACT OF THE DISSERTATION OF

Tiffany Lee van Huysen for the degree of Doctor of Philosophy in Forest Science presented on March 18, 2009.
Title: Nitrogen and Phosphorus Dynamics during Decomposition of Multiple Litter Types in Temperate Coniferous Forests.

Abstract approved:

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Mark E. Harmon Steven S. Perakis

Litter nutrient dynamics contribute significantly to biogeochemical cycling in forest ecosystems. These dynamics may be influenced by site attributes, litter nutrient concentrations, and soil nutrient availability either independently or synergistically. Litter nutrient dynamics were examined in two decomposition studies in temperate coniferous forests of Oregon. I used ^{15}N-labelled litter of three species in a comparative study of how site environment and initial substrate quality influence decomposition and nitrogen (N) dynamics of fresh foliage, fine roots, and twigs at Cascade Head Experimental Forest and H. J. Andrews Experimental Forest. There were no site differences with respect to N dynamics, and N mineralization patterns were species-specific. Although N immobilization did occur early in the decomposition process, the general trend for all litter was net N mineralization throughout the study without a net N immobilization phase. For several litter × species combinations the difference between gross N mineralization and net N

mineralization was significant, with gross N mineralization ~7 to 20% greater than net mineralization. These results suggest that initial litter chemistry is a more important driver than site environmental differences of the N dynamics associated with decomposition. I also assessed whether litter phosphorus (P) concentrations and soil P availability influenced decomposition rates and litter nutrient dynamics in N-rich Douglas-fir forests in the Oregon Coast Range using a factorial P fertilization experiment. Over the course of 2 years, fresh foliage, fine root, and twig litter from Douglas-fir seedlings were decomposed at three sites. Litter mineralized P at a rapid rate early in the decomposition process compared to N, which was mineralized more slowly or immobilized. Decomposition rates and mineralization of N and P were strongly correlated with initial litter chemistry. Initial litter element ratios between control and P-fertilized litter differed, but over the 2 years element ratios (C:N, C:P, N:P) converged to similar values across treatments. These studies confirm that net mineralization of N and P may occur early in the decomposition process and that litter may decompose without exhibiting a net N immobilization phase. Further, initial litter nutrient concentrations and element ratios may be important predictors of nutrient transformations during decomposition.

Nitrogen and Phosphorus Dynamics during Decomposition of Multiple Litter Types in Temperate Coniferous Forests

by
Tiffany L. van Huysen

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APPROVED:

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Co-Major Professor, representing Forest Science

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Co-Major Professor, representing Forest Science

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Head of the Department of Forest Science

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes the release of my dissertation to any reader upon request.

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Tiffany L. van Huysen, author

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DEDICATION

In loving memory of Dr. Elizabeth Sulzman—inspiring mentor, teacher, committee member, woman, athlete, friend.

NITROGEN AND PHOSPHORUS DYNAMICS DURING DECOMPOSITION OF MULTIPLE LITTER TYPES IN TEMPERATE CONIFEROUS FORESTS

CHAPTER 1: INTRODUCTION

Litter nutrient dynamics contribute significantly to biogeochemical cycling in forest ecosystems. Decomposition of litter is a key process that regulates the availability, retention, and loss of nutrients such as nitrogen (N) and phosphorus (P) within and from forested ecosystems. The rate at which decomposition occurs and the patterns of the associated litter N and P dynamics are controlled by multiple factors acting on different temporal and spatial scales. Examining these factors and how they influence N and P transformations during decomposition is important for understanding the fluxes of these elements, as both of these elements are essential for plant growth and productivity.

N is an essential element for plants and has important biochemical functions, namely as a constituent of amino acids, amides, proteins, nucleic acids, nucleotides, and coenzymes (Taiz and Zeiger 2002). In general, plants take up N in the form of ammonium (NH_4^+) or nitrate (NO_3^-), although there is evidence that plants are able to take up organic forms of N as well (Nasholm et al. 1998, Finzi and Berthrong 2005). Ammonium becomes available for plant uptake by either 1) biological N fixation (the major pathway by which atmospheric molecular N (N_2) enters the biogeochemical cycle), or 2) through decomposition of organic matter and the subsequent mineralization of nitrogenous compounds (Taiz and Zeiger 2002). Nitrate can enter the biogeochemical cycle through lightning fixation or photochemical fixation, both which produce nitric acid (HNO_3) that falls to Earth in rain. However, these two processes account for only about 10% of atmospheric N that is fixed (Taiz and Zeiger

2002). The majority of NO_3^- available for plant uptake comes from the recycling and nitrification of N compounds that enter soils through the decomposition of organic matter. Overall, internal recycling of ecosystem N is the primary source of plant available N in forest ecosystems, particularly as forests age (Turner 1977).

P is also essential for plant growth and is a key component of sugar phosphates, nucleic acids, coenzymes, and phospholipids. It is also a component of nucleotides that make up ATP, and thus is important for plant metabolism, as well as nucleotides that make up DNA and RNA (Taiz and Zeiger 2002). P differs from carbon (C) and nitrogen (N) in that its primary source is not the atmosphere and its availability in soils is primarily controlled by geochemical, rather than biological reactions (Chapin et al. 2002). The major input of P to ecosystems comes from the weathering of primary minerals, mainly calcium apatite (Walker and Syers 1976, Crews et al. 1995). This weathering releases P which either enters the organic P pool through uptake by organisms, or is sorbed onto the surface of secondary minerals (Crews et al. 1995). Over millennia, the dissolution of secondary silicate minerals from soils gives way to Al and Fe oxides, which have a strong affinity for P (Brady and Weil 1996, Chapin et al. 2002) . Thus, sorbed P will remain labile for a period of time, but if not taken into the organic P pool will eventually become occluded by Al and Fe hydrous oxides (Uehara and Gillman 1981, Chapin et al. 2002). Ultimately, continued weathering of P-containing primary minerals coupled with increasing concentrations of Al and Fe oxides over time leads to a decline in soil P availability (Walker and Syers 1976, Crews et al. 1995, Chapin et al. 2002). In ecosystems with

low soil P-availability, P is tightly cycled between plants and organic matter such that most of the available P remains in the organic P pool rather than entering the soil pool where it may complex with other ions or sorb to minerals as described above (Crews et al. 1995, Chapin et al. 2002). However, despite this tight cycling of P, studies have shown that ecosystems with low soil P-availability may still experience P-limitation of above- and belowground net primary productivity as well as decomposition rates (Vitousek and Farrington 1997, Hobbie and Vitousek 2000, Ostertag 2001, Cleveland et al. 2002). Further, some studies suggest that soil P availability may influence litter nutrient dynamics during decomposition (Ostertag and Hobbie 1999, Hobbie and Vitousek 2000, Ostertag 2001, McGroddy et al. 2004, Cleveland et al. 2006).

In addition to soil nutrient availability, it is also important to consider how decomposition rates and litter nutrient dynamics may be affected by initial litter nutrient concentrations. The results regarding the relationship between litter nutrient concentrations and decomposition rates are mixed (Hobbie and Vitousek 2000, Prescott et al. 2004). Further, there are few studies that have examined the effect of increased litter nutrient concentrations on decomposition rates. However, initial litter nutrient concentrations, particularly N and P, do seem to have a strong effect on litter nutrient dynamics (Hobbie and Vitousek 2000, Chen et al. 2002, Parton et al. 2007). Recent evidence suggests that N release from decomposing foliage can be predicted from initial N concentrations (Parton et al. 2007) and that initial litter N:P may predict patterns of P release or immobilization during decomposition (Moore et al. 2006)

Decomposition is an important process that regulates nutrient cycling, primary production and ecosystem carbon (C) storage, and is critical to the formation of soil organic matter (Hobbie and Vitousek 2000, Chapin et al. 2002). Hence, it is a key component of biogeochemical cycles and represents an important feedback process at both the plant and ecosystem levels. This process influences N and P availability and is regulated by the integration of geochemical and biochemical properties as well as biological activity in the soil. Thus, site characteristics (e.g., temperature, moisture, soil properties such soil type, soil ion exchange capacity, soil pH), plant species (through litter quality), and microbial activity may be important factors influencing ecosystem nutrient dynamics (Meentemeyer 1978, Melillo et al. 1982, Taylor et al. 1989, Hobbie et al. 2000, Hobbie and Vitousek 2000). Further, there is evidence suggesting that soil nutrients may influence decomposition in some ecosystems, particularly with respect to N and P (Hobbie and Vitousek 2000).

This dissertation explores the litter nutrient dynamics associated with the decomposition of multiple litter types in temperate coniferous forests of western Oregon. The objectives of this dissertation were to examine patterns of N mineralization from decomposing litter with respect to differences in site, initial litter chemistry, and P availability. Chapter 2 addresses N dynamics during decomposition at two sites using ^{15}N-labelled litter of multiple types and species representing a range of litter chemistries. Specifically, this chapter considers: 1) how site environment and initial litter chemistry influence mass loss and N dynamics of foliage, fine roots, and twigs, 2) whether N is mineralized from litter in the early phases of decomposition,

and 3) the degree to which N immobilization and mineralization exist simultaneously during the decomposition process. Chapter 3 considers whether P availability serves as a proximate control over mass loss dynamics and litter nutrient dynamics. Specifically, this chapter addresses the relationship between litter P content and soil P content with respect to decomposition rates and N mineralization during decomposition of multiple litter types.

These comparative analyses of litter decomposition set up a framework within which to examine the foliage-centric view of decomposition N dynamics. Further, these studies test ideas concerning the relationships between environmental factors, initial litter chemistry, soil nutrient availability, and element ratios with respect to N mineralization patterns during decomposition. In addition, this work addresses whether P may have an important, overlooked role in litter mass loss and nutrient dynamics. Understanding these relationships is fundamental to obtaining more complete view of the biogeochemical cycling of N in these forested systems and how N cycling may be impacted by future changes in climate or forest management practices.

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CHAPTER 2:
NITROGEN DYNAMICS DURING DECOMPOSITION IN TEMPERATE CONIFEROUS FORESTS: A COMPARATIVE ANALYSIS USING ^{15}N-LABELED LITTER

ABSTRACT

Litter nutrient dynamics contribute significantly to biogeochemical cycling in forest ecosystems. I used ^{15}N in a comparative study of multiple litter types to examine how site environment and initial substrate quality influence decomposition and nitrogen (N) dynamics of fresh litter (foliage, fine roots, and twigs). A 2.5 year time-series decomposition study was installed at Cascade Head Experimental Forest and H. J. Andrews Experimental Forest in Oregon using ^{15}N-labeled litter of bigleaf maple, Douglas-fir, and Sitka spruce. Mass loss for foliage was similar between the two sites, while roots and twigs had greater mass loss at Cascade Head than at H.J. Andrews. Twigs lost the least mass, whereas either foliage or roots exhibited the most mass loss depending on the site or species. Species differences in mass loss were more prominent at Cascade Head. Initial N content values ranged from 1.00-1.37% for foliage, 1.04-1.17% for roots, and 0.62-0.82% for twigs. There were no site differences with respect to litter N dynamics and litter N mineralization patterns were species-specific. Although some individual samples exhibited N immobilization early in the decomposition process, the general trend for all litter types was N mineralization throughout the study. For several litter × species combinations the difference between gross N mineralization and net N mineralization was significant, with gross N mineralization ~7 to 20% greater than net N mineralization. Although differences between the two sites were important for mass loss, these results suggest

that for these two sites initial litter chemistry is a more important driver of the N dynamics associated with decomposition than site environmental differences. The results for gross and net mineralization demonstrate that greater amounts of N are cycling through these systems than can be quantified when only considering net N mineralization and that litter in the early phases of decomposition may contribute a significant amount of N to forested systems.

INTRODUCTION

The decomposition process is a key component of the biogeochemical N cycle and represents an important feedback process at both the plant and ecosystem levels. This process influences N availability and is regulated by the integration of such factors as geochemical and biochemical properties as well as biological activity in the soil. Thus, site characteristics (e.g., temperature, moisture, soil properties such soil type, soil ion exchange capacity, soil pH), plant species (through litter quality), and microbial activity may be important factors influencing ecosystem N dynamics through their effects on decomposition (Meentemeyer 1978, Melillo et al. 1982, Taylor et al. 1989, Hobbie et al. 2000, Hobbie and Vitousek 2000).

A large proportion of the work on nutrient dynamics associated with decomposition has examined senesced leaf litter. From this large body of work on leaf litter decomposition, a general pattern of the associated N dynamics has emerged. Generally, leaf litter tends to immobilize N early in the decomposition process (resulting in an N content in the litter higher than the initial N content) and tends to mineralize N during later phases of decomposition (Gosz et al. 1973, Staaf and Berg

1982, Hobbie and Vitousek 2000, Parton et al. 2007). However, leaf litter with high initial N concentrations may be an exception to this pattern and mineralize N early in the decomposition process (Parton et al. 2007).

Comparatively, there is less knowledge with respect to the decomposition and nutrient dynamics of other litter types (e.g. fine roots and twigs) and the feedbacks that may occur at the plant and ecosystem levels as a result of this decomposition. However, there is evidence suggesting that fine root litter may also be an exception to the pattern of N immobilization followed by mineralization and may mineralize N even in the earliest phases of decomposition (Silver and Vogt 1993, Chen et al. 2001, Chen et al. 2002, Dornbush et al. 2002, Silver et al. 2005, Parton et al. 2007). While multiple factors are important in regulating decomposition (as described above), the initial N concentration of litter has emerged as an important driver of the degree to which litter immobilizes or mineralizes N and the timing of these processes (Chen et al. 2002, Parton et al. 2007).

When attempting to identify patterns of N mineralization and quantify the amount of N being immobilized or mineralized during decomposition, it is important to distinguish between net and gross transformations of N. Similar to soil studies, the rates of N mineralization from decomposition studies are generally net rates that do not account for the multiple transformations taking place (Hart and Myrold 1996, Chen et al. 2002, Parton et al. 2007). Consequently, net rates or net amounts of N mineralization may underestimate the total amount of N cycling through an ecosystem. As for soil studies, application of methods using the stable isotope ^{15}N is

an approach that can be used to examine the N transformations occurring during the decomposition of litter (Hart and Myrold 1996). This approach can be used to study the processes of N immobilization and mineralization as well as to determine the fate of N mineralized from litter (Zeller et al. 2000, Zeller et al. 2001). Further, by using ^{15}N it is possible to distinguish between net and gross transformations of N and account for net and gross fluxes of N within a system. Understanding these processes provides insight into the contributions of decomposing litter to ecosystem N dynamics. I used ^{15}N-labeled litter in a field time series study in temperate coniferous forests of western Oregon to examine N dynamics during litter decomposition. More specifically, I evaluated: 1) how site environment and initial litter chemistry influenced mass loss and N dynamics of foliage, fine roots, and twigs, 2) whether N is mineralized from litter in the early phases of decomposition, and 3) the degree to which N immobilization and mineralization exist simultaneously during the decomposition process. This comparative analysis of litter decomposition allowed me to re-examine the foliage-centric view of N dynamics by also providing insight on roots and twigs. Further, by using ^{15}N, I was able to describe both net and gross N mineralization associated with decomposing litter and thus offer a more complete view of the amount of N cycling through these forested systems.

METHODS

Site description

I conducted this research at Cascade Head Experimental Forest and H. J. Andrews Experimental Forest in western Oregon. Cascade Head Experimental Forest

(45º12’ N, 123º12’ W) is located on the Pacific coast near the town of Otis. This region has a maritime climate, with a mean annual temperature of 10°C and a mean annual precipitation of 245 cm. The dominant forest type from the coast to ~3 km inland is a mixture of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and also includes Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), red alder (*Alnus rubra* Bong.) and western redcedar (*Thuja plicata* Donn ex. D. Don). The soils are silt loams to silty clay loams derived from marine siltstones. They are moderately well-drained and high in organic matter and N. H. J. Andrews Experimental Forest (44°12’ N, 122°12’ W) is located 80 km east of the city of Eugene on the west slope of the Cascade Range. This region also has a maritime climate, with a mean annual temperature of 8.5°C and a mean annual precipitation of 230 cm at lower elevations and 355 cm at higher elevations. Winters are wet and mild and summers are dry and cool. At low elevations, the forests are dominated by Douglas-fir and western hemlock (Franklin and Dyrness 1973). Soils are deep, well-drained Andisols. At each site, three plots representative of the site’s forest composition were established for the litter decomposition experiment (Table 2.1). See Figure 3.1 for monthly precipitation and temperature data for the duration of the study.

Soil chemistry

Soil N and P availability was measured using ion exchange resin bags. Resin bags consisted of 20 g of anion exchange resin (Biorad AG-1X8 Resin, Cl^-, 20-50 dry mesh, 300-1180 μm wet bead) or 20 g of cation exchange resin (Biorad AG50W-X8

Resin, H^+, 20-50 dry mesh, 300-1180 μm wet bead) in un-dyed nylon stockings. At each plot, 6 pairs of anion/cation resin bags were strung on nylon string and then buried at a depth of 10 cm by insertion into a narrow slit in the ground, with the resin bag pairs 1 m apart. Resin bags were collected and new resin bags were installed every 3 months for the duration of the study.

Prior to analysis, litter and soil adhering to the resin bags were brushed off. The bags were rinsed once with deionized water to remove any remaining soil and then spun dry in a salad spinner. The resins were then extracted in a specimen cup with 200 mL 2M NaCl in 0.1 M HCl, shaken for 1 hour and then filtered through pre-rinsed Whatman 42 filter paper in funnels into 20 mL scintillation vials. Extracts were analyzed immediately or frozen until analysis. Extracts were analyzed for NH_4^+-N colorimetrically using the salicylate method (QuikChem Method 12-107-06-2-A, Lachat Instruments, Milwaukee, WI, USA). Extracts were analyzed colorimetrically for NO_3^--N using the cadmium reduction method (QuikChem Method 12-107-04-1-F, Lachat Instruments, Milwaukee, WI, USA) using a 50 cm sample loop. Extracts were analyzed colorimetrically for PO_4^{3-}-P using the molybdate blue method (QuikChem Method 12-115-01-1-A, Lachat Instruments, Milwaukee, WI, USA), except the analysis was run at 45°C with an 880 nm interference filter.

I sampled the mineral soil at each site in August, 2008 to obtain general background soil data. After removal of surface litter, four soil cores were collected randomly to a depth of 10 cm from each plot at each site using a 6.7 cm diameter steel corer. Two cores from each plot were composited in a polyethylene bag (for a total of

6 samples for each site) and kept on ice for transport bag to the lab. Prior to analysis, composited samples were sieved to 2 mm. The < 2 mm fraction was used for all subsequent soil analyses. Gravimetric soil moisture content was determined by drying a 10 g subsample of soil for 48 h at 105°C. Soil pH was determined in a 2:1 mixture of deionized water:field-moist soil, with supernatant pH measured after 30 minutes equilibration using an Accumet pH meter with a glass-body combination probe (Fisher Scientific, Hampton, NH, USA).

Extractable NH_4^+-N, NO_3^--N, TN and TC were determined in a 7 g subsample of field-moist soil extracted with 35 mL of 0.5M K_2SO_4. Samples were shaken for 1 h, allowed to settle for 30 min, and then filtered through pre-rinsed Whatman 42 filter paper in funnels into 20 mL polyethylene scintillation vials. Extracts were analyzed immediately or frozen until analysis. Extracts were analyzed for NH_4^+-N colorimetrically using the salicylate method (QuikChem Method 12-107-06-2-E, Lachat Instruments, Milwaukee, WI, USA). Extracts were analyzed colorimetrically for NO_3^--N using the cadmium reduction method (QuikChem Method 12-107-04-1-H, Lachat Instruments, Milwaukee, WI, USA). Extracts were analyzed for dissolved organic carbon (DOC) and total dissolved N (TDN) by catalytic oxidation combustion using a Shimadzu TOC-V CSH total organic carbon analyzer with a TNM-1 total N measuring unit (Shimadzu Scientific Instruments, Columbia, MD, USA). To determine chloroform-labile microbial C and N ($CHCl_3$-C and $CHCl_3$-N), a second set of soil subsamples was fumigated with chloroform using the chloroform-direct-extraction method (Davidson et al. 1989). Soil samples were placed in a dessicator

lined with wet paper towels along with a flask of ~50 mL chloroform. The dessicator was evacuated 3 times, allowing the chloroform to boil for 2 minutes on the first evacuation. At the end of the 3rd evacuation, the dessicator was sealed. Samples were incubated in the dark at room temperature (~25°C) for 24 h, allowed to vent to the atmosphere for 10 minutes, and then extracted and analyzed as above for TC and TN.

Extractable P was determined by acid-fluoride extraction (Bray and Kurtz 1945). Twenty-five mL extractant (NH_4F-HCL) was added to a 5 g subsample of field-moist soil in a centrifuge tube. Samples were shaken by hand for 1 min and then centrifuged for 5 min at 3400 rpm (IEC multi centrifuge, Thermo Electron Corporation, Milford, MA, USA). The supernatant was then filtered through Whatman 42 filter paper into 20 mL polyethylene scintillation vials. Extracts were analyzed immediately or frozen until analysis. Extracts were analyzed using the molybdate blue colorimetric method for ortho-phosphate (QuikChem Method 12-115-01-1-A, Lachat Instruments, Milwaukee, WI, USA). To determine chloroform-labile microbial P ($CHCl_3$-P), a second set of soil subsamples was fumigated with chloroform using the chloroform-direct-extraction method described above. Fumigated samples were extracted and analyzed as above for ortho-phosphate. Determination of DIN, DON, and microbial biomass C, N, and P is described in Calculations and statistical analyses. Blanks were collected for all soil extractions using the same methods as used for the soil samples. For blanks, no soil was added to the containers used for extractions. Blanks were analyzed as above with the corresponding soil extracts.

For total C and N, approximately 20 g subsamples of field-moist soil were dried at 65°C for 72 h and ground to a powder on a roller mill (~2 h). Tin capsules were filled with 12 g of ground soil and analyzed for total C and N against an Atropine standard on a Costech ECS-4010 elemental combustion analyzer (Costech Analytical, Valencia, California, USA).

Decomposition and litter chemistry

Two-year-old seedlings of bigleaf maple (*Acer macrophyllum* Pursh.), Douglas-fir, and Sitka spruce obtained from a local nursery were planted in 1-gallon (Douglas-fir and Sitka spruce) or 2-gallon (bigleaf maple) pots of peat with one seedling per pot. Seedlings were maintained in an open-air greenhouse and fertilized with 6.25 g N m^{-2} using a $^{15}NO_4{}^{15}NO_3$ (99 atom%) solution, applied four times from May to September 2003. Seedlings were harvested in the following manner: 1) seedlings with peat-bound roots intact were removed from the pots 2) peat was removed by hand, 3) root masses were separated from aboveground biomass by clipping the main stem, 4) root masses were rinsed to remove any remaining peat, and 5) the ^{15}N-labeled litter was allowed to air dry. Once dry, litter of each type (foliage, roots, and twigs) from each species was composited and 5 g subsamples of litter were placed in mesh litter bags. Root and twig samples from each species were placed in 1-mm nylon mesh bags. Foliage samples from each species were put in litter bags with 1-mm nylon mesh tops and 55 µm Dacron mesh bottoms (referred to as "mesh" bags). An additional set of 55-µm Dacron mesh litter bags (referred to as "cloth" bags) were also filled with litter of each type from each species as a comparison to the larger

mesh size litter bags. Litter bags were sealed using staples and labeled with a uniquely numbered aluminum tag. Subsamples of initial litter from the seedlings were retained to analyze for moisture content, lignin, total C and N, and ^{15}N.

Litter bags to be collected at a particular date were strung together using nylon string. Each string held either 9 (3 litter types x 3 species) mesh bags or 9 cloth bags. Two strings (replicates) for each collection were placed in each plot at each site in May 2004. Litter bags were 1 m apart, with the order of the bags on the strings randomized. Mesh litter bags containing root samples were buried at a depth of 10 cm. All cloth bags were buried at a depth of 10 cm. Mesh litter bags were collected at 0.25, 0.5, 0.75, 1, 1.5, 2, and 2.5 years after initial placement. Cloth bags were collected at 0.25, 1, and 2.5 years. An additional set of mesh litter bags (referred to as "buried mesh") containing foliage or twigs of bigleaf maple or Sitka spruce were buried and collected at 0.25, 1, and 2.5 years as a comparison for litter left aboveground to decompose. There was not enough Douglas-fir litter to include in this additional set. In the field at each collection, litter bags were carefully cleaned of moss, in-growing roots, and soil and then transported back to the lab on ice. Litter was then removed from the litter bags, gently brushed free of soil, dried to a constant mass at 65ºC, and weighed. After drying and weighing, replicate litter samples were composited for subsequent analyses.

Dried litter samples were coarse ground on a Cyclotec 1093 Sample Mill (Rose Scientific Ltd., Edmonton, Alberta, Canada) and roller milled to a powder. Ground litter subsamples (6 mg) were weighed into tin capsules and analyzed for total C, N

and ^{15}N at the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University. Due to the cost of isotope analysis, only litter subsamples from mesh bags collected at 0.25, 1, and 2.5 years were analyzed for total C and N and ^{15}N. To determine ash-free dry mass (AFDM), 1 g subsamples of dried litter were ashed in a muffle furnace for 4 h at 500ºC. Initial litter samples were dried, ground, and analyzed for total C and N and ^{15}N as above. Lignin content of initial samples was assayed using the acid detergent method at the University of Nebraska-Lincoln Soil and Plant Analytical Laboratory (Lincoln, NE, USA).

CALCULATIONS AND STATISTICAL ANALYSES

The statistical software package SAS 9.1 (SAS Institute, Cary, NC, USA) was used for all analyses except Monte Carlo simulations (described below). Prior to analysis, normal probability plots were used to check data distributions for normality and residual plots were used to check for homogeneity of variances. Log transformations were applied when necessary. Results were considered significant at $P < 0.05$. For a list of the ANOVA mixed models and their associated effects used for the comparisons above, see Table A1.1.

Resin soil N and P availability

Due to low levels of NO_3^- in resin extracts, many values fell below the detection limit of 0.1 mg NO_3^--N L^{-1}. These were assigned a value of 0.05 mg L^{-1}. Resin NH_4^+-N, NO_3^--N, and PO_4^{3-}-P were compared using a mixed effects model with repeated measures (PROC MIXED in SAS 9.1). Fixed effects were site, time, and site

× time. The random effect was plot (site), where site is nested within plot. The subject of the repeated measures was plot × site × collection.

Mass loss dynamics and decomposition rates

Mass loss is expressed as percent of initial litter mass remaining for all species, litter types, and litterbag types and was calculated using ash-corrected litter mass values:

(1) $$PMR = (M_t / M_i)*100$$

where PMR is percent of initial mass remaining, M_t is litter mass for a given collection time, and M_i is initial litter mass. Since dried litter samples were composited, the PMR values presented are the average PMR values for the two replicate samples collected at a given time. Analysis of variance (ANOVA) was used to compare PMR for each site × plot × species × litter combination for mesh litterbags using a mixed effects model with repeated measures (PROC MIXED in SAS 9.1). Fixed effects were site, species, litter, time, and all interactions between these effects. The random effect was plot (site), where site is nested within plot. The subject of the repeated measures was plot × site × species × time. PMR was compared between mesh and cloth litterbag types using a mixed effects model with repeated measures (PROC MIXED in SAS 9.1). Fixed effects were site, species, litter, bag, time, and all interactions between these effects. The random effect was plot (site), where site is nested within plot. The subject of the repeated measures was plot × site × species × bag × time. The same model used to compare PMR between mesh and cloth litterbags was used for PMR comparisons between mesh and buried mesh litterbags.

Decomposition rates were only calculated for litter from mesh bags. Because litter from cloth and buried mesh bag types was only collected at three time points there was insufficient mass loss data to calculate reliable decomposition rates based on the double-exponential decomposition model that was used for the mesh bags (see below). For litter from mesh bags, PMR data was converted to proportion of mass remaining by dividing by 100 (e.g. PMR of 100 equals proportion of mass remaining of 1). The proportion of mass remaining data was transformed to the natural logarithmic scale resulting in a value of zero for the initial mass on the log scale. This value of zero represents the y-intercept. Linear regression (PROC REG in SAS 9.1) was then used to test whether the intercepts for regression lines fitted to the log-transformed proportion data were significantly different from zero. This test was used to determine whether linear or non-linear regression was appropriate for analyzing the PMR data and calculating decomposition rate constants. If the intercept of the regression line was significantly different from zero ($P<0.05$), then non-linear regression was used to describe mass loss dynamics. Except for Douglas-fir roots, all litter species and types had intercepts significantly different from zero. Douglas-fir root PMR data were still analyzed using non-liner regression to allow for comparisons across all species and litter types.

Based on the results of the intercept test described above, non-linear regression in the form of a double-exponential decomposition model (PROC NLIN in SAS 9.1) was used to describe the mass loss dynamics of litter decomposed in the mesh bags. The double-exponential regression model is:

(2) $$PMR = F_{slow}e^{-k_{slow}t} + (100 - F_{slow})e^{-k_{fast}t}$$

where PMR is percent initial mass remaining, F_{slow} is the slowly decomposing litter fraction, k_{slow} (yr^{-1}) is the decomposition rate of the slow fraction, k_{fast} (yr^{-1}) is the decomposition rate of the fast fraction, t is time (years), and e is the exponential function or the base of the natural logarithm. The fast fraction (F_{fast}) is equivalent to the model term 100-F_{slow}. This model results in estimates of F_{slow}, k_{slow}, F_{fast}, and k_{fast} for each site × plot × species × litter type combination. Comparisons of the estimates from the double exponential model between site × species × litter type combinations were made using a mixed effects model with repeated measures (PROC MIXED in SAS 9.1). Fixed effects were site, species, litter, site × species, site × litter, species × litter, and site × species × litter. The random effect was plot (site), where site is nested within plot. The subject of the repeated measures was plot × site × species.

The original PMR data (expressed as proportion of mass remaining) and the estimates obtained from the double-exponential regression were used to predict what are referred to as "integrated *k*" values (Harmon, personal communication). An integrated *k* value represents what the *k* value, or decomposition rate constant, would be when the litter pool reaches steady-state (i.e. when inputs to the fast and slow decomposition pools are equivalent to the losses from these pools). The mass of the litter pool at steady-state (M_{ss}) is represented by the following equation:

(3) $$M_{ss} = (F_{slow}/k_{slow}) + (F_{fast}/k_{fast})$$

where F_{slow}, k_{slow}, F_{fast}, and k_{fast} are the parameters from the double-exponential regression model as described above. The litter pool steady-state mass (M_{ss}) can then be used to calculate the integrated *k* value:

(4) $$\text{integrated } k = 100/M_{ss}$$

where 100 is the total input.

SAS 9.1 was used to calculate the area under the regression curve resulting from the double-exponential parameter estimates for a 0.1 year time interval for each site × plot × species × litter combination and accounting for the previous year and current year PMR. This was repeated for total of 500 years (the time it took for all litter types to reach steady-state). A running total of the calculated area was kept throughout the simulation. This area, which represents the mass of the litter pool (M_{ss}), was then used to calculate the integrated *k* value for each site × plot × species × litter type using Equation 4 from above.

Integrated *k* values were compared using the same mixed model as above for the comparisons of the double-exponential model estimates. Monte Carlo simulations from repeated samplings of the double-exponential parameter estimates were used to estimate an integrated *k* value and its associated uncertainty for each site × litter type × species combination using the software R 2.8.0 (R Development Core Team). For each combination there were 10,000 samplings.

To obtain *k* values for the actual time interval of this study (2.5 years), a different calculation was used to estimate what I term "single exponential equivalent *k*" values (k_e). This calculation, based on numerical approximation, keeps a running total of the

area under the decomposition curve and then derives the k_e value for each site × plot × species × litter combination that would result in this calculated area if decomposition did follow a negative single exponential curve. The total area under the curve is the sum of rectangular divisions that correspond to PMR data (expressed as proportion of mass remaining) for given times and the k_e value is then estimated as the inverse of the total area. In contrast to the integrated k values, the k_e values are not steady-state decomposition rates as they only represent the rates for 2.5 years of decomposition. Values for k_e were compared using the same mixed model as for the double-exponential model estimates and integrated k values.

Litter chemistry and N dynamics

Initial litter C, N, and lignin content were analyzed statistically using separate two-way ANOVAs with species and litter as main effects and including the species × litter interaction (PROC GLM in SAS 9.1). A Tukey adjustment was used for multiple comparisons.

The following equation was used to calculate the ^{15}N isotope ratio of the initial litter:

(6) $$R_{initial} = R_{standard} * ((\delta^{15}N_{initial} + 1000)/1000)$$

where $R_{initial}$ is the $^{15}N/^{14}N$ isotope ratio of the initial litter for a given species and litter type, $R_{standard}$ is the isotope ratio of the standard (air, 0.0036765), and $\delta^{15}N_{initial}$ is the measured ^{15}N content of the initial litter for a given species and litter type.

The $\delta^{15}N_{initial}$ and calculated $R_{initial}$ values from Equation 6 were then used to calculate gross N mineralization as follows:

(7) $$\text{Gross N mineralization} = (\delta^{15}N_{initial} - {}^{15}N_t)/ R_{initial}$$

where ${}^{15}N_t$ is the measured content of a litter sample for a given collection time (0.25, 1, or 2.5 years).

Net N mineralization was calculated as the difference between initial N content and N content for a given collection time:

(8) $$\text{Net N mineralization} = N_{initial} - N_t$$

N uptake was then calculated as follows:

(9) $$\text{N uptake} = N_{gross} – N_{net}$$

where N_{gross} is gross N mineralization and N_{net} is net N mineralization for a given species, litter type, and collection time from Equations 7 and 8.

Equations 7, 8, and 9 give N mineralization or uptake values for time intervals from 0 to time t express results as percent of initial N remaining or mineralized.

Gross N mineralization for each site × plot × species × litter combination for the duration of the study (2.5 years) was compared using a mixed effects model with repeated measures (PROC MIXED in SAS 9.1). Fixed effects were site, species, and litter, and all interactions between these effects. The random effect was plot (site), where site is nested within plot. The subject of the repeated measures was plot × site × species. The same model used to compare gross N mineralization was used for net N mineralization comparisons and total N uptake comparisons at 2.5 years. Gross N mineralization, net N mineralization, and N uptake for each time interval (0 to 0.25 years, 0.25 to 1 year, 1 year to 2.5 years) were compared using a similar model, with the addition of time as a fixed effect and to the subject of the repeated measures.

Because results for N dynamics indicated no site differences, differences between gross and net N mineralization were tested for significance using a single-sample t-test on the difference for each species × litter combination averaged over site ($\alpha = 0.05$).

I explored the relationships between initial N concentration and gross and net N mineralization by applying equations used to model patterns of N release during leaf litter decomposition in the Long-Term Intersite Decomposition Experiment (LIDET) to my data (Parton et al. 2007). Relationships between initial litter chemistry (lignin, N content, C:N), decomposition (k_e values), and N dynamics (gross N release, net N release, N uptake) were explored using correlation.

The potential N inputs to soil in these systems with respect to the results of this study were calculated using estimates of annual litterfall (Grier and Logan 1977), foliage and root biomass (Campbell et al. 2004), and twig biomass (van Huysen, unpublished data) in Pacific Northwest forests. For foliage, the litterfall estimate includes litterfall for both conifers and hardwoods (Grier and Logan 1977). Equal litterfall estimates based on litter type were used for all species, rather than weighting the litterfall estimates by species, due to lack of information regarding relative contributions of species to root and twig litterfall and also to observe the differences in N inputs given equal masses of litter inputs per area and per year. Estimates of N mineralization from this study after one year of decomposition were then applied to the litterfall estimates to calculate the annual potential N inputs to soil given these litter inputs.

Foliage and root biomass estimates across age types from the Coast Range and western Cascades were used to calculate potential N inputs to these systems after a disturbance. This scenario assumes that the disturbance would cause complete mortality of all trees and that the resulting necromass would be left to decomposition. As for the litter input calculations, biomass estimates were not weighted by species and thus these calculations represent N inputs from disturbance to monospecific stands. Biomass estimates for twigs for these age types and ecosystems were obtained by applying a ratio of foliage biomass to twig biomass (van Huysen, unpublished data) to the foliage biomass data from Campbell et al. 2004 study.

RESULTS

Resin soil N and P availability

The two sites differed significantly in resin available NH_4^+-N and PO_4^{3-}-P, with greater NH_4^+-N at Cascade Head and greater PO_4^{3-}-P at H.J Andrews (Figure 2.2).. Resin NH_4^+-N ranged from 3-10 $\mu g \cdot g^{-1}$ wet resin at Cascade Head and from 3-7 $\mu g \cdot g^{-1}$ wet resin at H. J. Andrews. Resin PO_4^{3-}-P ranged from 3-60 $\mu g \cdot g^{-1}$ wet resin at Cascade Head and from 19-294 $\mu g \cdot g^{-1}$ wet resin at H. J. Andrews. Resin NH_4^+-N differed significantly with respect to the interaction of site × time ($P < 0.01$). There were no significant differences for NO_3^--N and values ranged from 0.05-0.3 $\mu g \cdot g^{-1}$ wet resin at both sites. Site and time ($P < 0.01$ for both effects) were also significant for resin PO_4^{3-}-P. Additional background soil data is available in Table 2.2; resin data is available in Table A1.2.

Mass loss dynamics and decomposition rates

Due to the significance of multiple effects (site × litter: $P < 0.01$, species × litter: ($P < 0.01$), species × litter × time: ($P < 0.01$), PMR for mesh litterbags exhibited few general trends for specific litter types or species (Table A1.3). For both sites, foliage had the lowest PMR at the end of the study and twigs had the highest, but roots exhibited the lowest PMR values early in the study. Bigleaf maple roots had the lowest PMR values for the last collection whereas foliage had the lowest values for Douglas-fir and Sitka spruce. Bigleaf maple and Sitka spruce had similar differences in PMR between litter types. Douglas-fir, however, exhibited smaller differences in PMR between roots and twigs, particularly early in the study (Figure 2.3). After 2.5 years, PMR (as % of initial mass) for mesh litterbags ranged from 31-58% (foliage), 41-53% (roots), and 47-67% (twigs).

For PMR comparisons between mesh and cloth litterbags, multiple interactions were significant (Table A1.4). PMR was slightly greater for mesh litter bags than cloth bags (Figure 2.4) for each collection, indicating slower decomposition for litter decomposing in mesh litterbags. Multiple interactions were also significant for the comparison between mesh and buried mesh litterbags (Table A1.5). PMR (as % of initial mass) for cloth litterbags at the end of the study ranged from 21-63% for foliage, 44-60% for roots, and 47-68% for twigs. PMR was greater for mesh than for buried mesh litterbags, indicating slower decomposition for bigleaf maple and Sitka spruce foliage and twig litter decomposing aboveground in mesh litterbags compared to decomposing belowground in the buried mesh litterbags (Figure 2.5). PMR for

buried mesh litterbags after 2.5 years ranged from 17-40% and 35-46% for foliage and twigs, respectively.

When decomposition rates were fitted with the two-pool model, the two sites did not differ in the amount of litter mass decomposing in the fast and slow pools or the decomposition constants associated with these pools (Figure 2.3). Foliage had a greater proportion of its mass decomposing in the fast pool than roots or twigs, respectively (litter type: $P = 0.01$ for both pools). Litter decomposing at H.J. Andrews exhibited larger k_{fast} values (faster decomposition within the fast pool) than Cascade Head litter, although there were no significant differences for k_{fast} with respect to any of the fixed effects. Values for k_{fast} ranged from 4-11 yr^{-1} (foliage), 3-15 yr^{-1} (roots), and 2-15 yr^{-1} (twigs). The litter × species interaction was significant for comparisons of k_{slow} ($P = 0.04$), with Sitka spruce twigs decomposing the slowest (smallest k_{slow} values) for the fraction of mass in the slow pool, followed by bigleaf maple foliage and Douglas-fir roots (highest k_{slow} values). Values for k_{slow} ranged from 0.05-0.3 yr^{-1} (foliage), 0.06-0.2 yr^{-1} (roots), and 0.06-0.2 yr^{-1} (twigs) (Table 2.3).

Integrated k values varied with respect to differences among litter types for the different species, with bigleaf maple litter exhibiting a different pattern than litter from the two coniferous species (litter × species: $P = 0.02$). For bigleaf maple, roots exhibited the largest integrated k values, followed by twigs and then foliage. Douglas-fir and Sitka spruce foliage had larger integrated k values than the roots or twigs of these two species. Overall, Sitka spruce foliage had the largest integrated decomposition constant and bigleaf maple foliage had the smallest integrated

decomposition constant. For foliage, integrated *k* values ranged from 0.07-0.3 yr^{-1}. Root and twig integrated *k* values ranged from 0.08-0.3 yr^{-1} and 0.07-0.2 yr^{-1}, respectively (Table 2.4). Integrated *k* values from the Monte Carlo simulations were similar to those calculated from the observed data with the exception of Sitka spruce foliage at H.J. Andrews, which exhibited large variability with respect to the estimates of the fast and slow pool fractions and thus a poorly-constrained estimate of integrated *k* (Table 2.4).

With respect to k_e values, the general pattern for both sites was that of foliage decomposing the fastest and twigs decomposing the slowest, with foliage decomposing ~1.5-2 times faster than twigs. There was a significant site × litter ($P < 0.01$) interaction driven by slightly higher k_e values (faster decomposition) for roots at H.J. Andrews. As for integrated *k*, there were differences in k_e values between litter types with respect to the different species (litter × species: $P < 0.01$). For bigleaf maple, roots exhibited the fastest decomposition, followed by foliage and twigs which were similar to one another. In contrast, foliage decomposed the fastest for Douglas-fir and Sitka spruce, followed by roots and then twigs. Sitka spruce foliage demonstrated the fastest decomposition, decomposing almost 3 times faster than Sitka spruce twigs, which decomposed the most slowly (Table 2.4). For multiple comparisons of integrated *k* values and k_e values see Table A1.6 and Table A1.7.

Litter chemistry and N dynamics

Initial chemistry varied among litter types and species (Table 2.5). Lignin was generally greatest in roots and Douglas-fir and lowest in foliage and bigleaf maple.

Lignin content ranged from 17-21% for foliage, 26-35% for roots, and 11-26% for twigs. Foliage tended to have the highest initial N concentrations and lowest C:N while twigs exhibited the opposite trends. Initial N concentrations and C:N were generally higher for the two coniferous species. Initial C concentrations ranged from 435-492 $mg \cdot g^{-1}$ litter for foliage, 456-469 $mg \cdot g^{-1}$ litter for roots, and 461-492 $mg \cdot g^{-1}$ litter for twigs. Initial N concentrations ranged from 10-14 $mg \cdot g^{-1}$ litter for foliage, 10-11 $mg \cdot g^{-1}$ litter for roots, and 6-8 $mg \cdot g^{-1}$ litter for twigs. For C:N, values ranged from 36-44 for foliage, 40-45 for roots, and 57-79 for twigs. All three initial litter chemistry variables (lignin content, N concentration, and C:N) differed significantly ($P < 0.01$) with respect to the interaction of litter × species.

All litter types and species lost N in the early phases of decomposition. Because there were no significant site differences for any comparisons of N dynamics in litter, results (% differences) presented below from the PROC MIXED models were based on the LSMEANS estimates for litter × species. Gross N and net N mineralization patterns over the course of 2.5 years were similar but these patterns differed for each litter type and species (litter × species: $P < 0.01$ for both gross and net mineralization) (Figure 2.6). For gross mineralization after 2.5 years, bigleaf maple roots mineralized the most N and foliage mineralized the least amount of N, with roots mineralizing 29% more N than foliage and 16% more N than twigs. Sitka spruce foliage mineralized 37% more N than roots and 64% more N than twigs. For Douglas-fir, twigs mineralized the most N, followed by foliage and then roots, with twigs mineralizing 10% and 24% more N, respectively. Overall, after 2.5 years of

decomposition, gross N mineralization (expressed as % of initial N) ranged from 29-73% for foliage, 39-58% for roots, and 9-58% for twigs (Table 2.6).

The pattern of net N mineralization across litter types and species was similar to the pattern for gross N mineralization (Figure 2.6). For net N mineralization, bigleaf maple roots mineralized 36% more net N than foliage and 3% more than twigs. Sitka spruce foliage mineralized 18% and 32% more net N than roots and twigs, respectively. For Douglas-fir, twigs mineralized 16% more net N than foliage and 18% more net N than roots.

The difference between gross N mineralization and net N mineralization at 2.5 years was significant for bigleaf maple foliage, bigleaf maple roots, Sitka spruce foliage, and Douglas-fir foliage and twigs (Table 2.6). For these species × litter combinations, gross N mineralization ranged from ~7%-20% more than net N mineralization. Net N mineralization (expressed as % of initial N) ranged from 8-36% (foliage), 33-45% (roots), and 19-52% (twigs) after 2.5 years (Table 2.6).

N immobilization differed with respect to litter ($P < 0.01$) and species × litter ($P = 0.03$). Bigleaf maple and Sitka spruce demonstrated similar patterns for total N uptake, with foliage taking up the most N and twigs the least (Figure 2.6). Bigleaf maple foliage took up 5% more N than roots and 18% more N than twigs, while Sitka spruce foliage took up 15% more N than roots and 31% more N than twigs. Douglas-fir foliage also took up the most N, but in contrast to bigleaf maple and Sitka spruce, the roots of this species took up the least amount of N and were similar to twigs in terms of N uptake. Douglas-fir foliage took up 7% more and 6% more N than roots

and twigs, respectively. Uptake (as % of initial) ranged from 13-20%, 6-14%, and -11-1% for foliage, roots, and twigs, respectively (Table 2.6). For ANOVA results for gross N mineralization, net N mineralization, and N uptake see Table A1.8. For multiple comparisons of gross N mineralization, net N mineralization, and N uptake see Tables A1.9, A1.10, and A1.11.

Gross N mineralization per time interval differed significantly only with respect to species × litter ($P < 0.01$). Net N mineralization per time interval, however, differed with respect to species × time × litter. Time × litter, and site × species × time were significant effects for N uptake per time interval (Table A1.12). Differences between gross mineralization and net mineralization per time interval varied with litter, species, and time. Foliage exhibited the most significant differences between gross mineralization and net mineralization per time interval, followed by roots and then twigs. With respect to species, Douglas-fir exhibited the most significant differences and Sitka spruce the least. The intermediate time interval (0.25-1 year) had the most significant differences of the three intervals (Table A1.13).

Predicted N mineralization patterns generated using the LIDET model underestimated N mineralization (both gross and net) when compared to data generated by this study (Figure 2.7). For all litter types and species, the LIDET model predicted a net N immobilization phase. This is in contrast to the data for this study, in which all litter types and species exhibited a pattern of N mineralization without a net N immobilization phase.

There were multiple significant correlations between decomposition rate constants or N dynamic variables and initial litter chemistry constituents for the different litter types. For foliage, k_e values and both gross and net N release were significantly correlated with initial lignin content, initial N content, and initial C:N ($P < 0.01$ for all variables). For roots, integrated k, k_e, and gross N release were significantly correlated with all three initial chemistry variables, but net N release and N uptake were only significantly correlated with initial N content and initial C:N. For twigs, there were significant correlations between integrated k, k_e, and net N release with all three chemistry variables. Gross N release for twigs was significantly correlated with only initial N and initial C:N, as was N uptake (Table A1.14).

Assuming equivalent amounts of litter input for all litter types and species considered, net and gross N inputs to the soil from decomposing litter in the first year would be greatest for foliage and roots. Net mineralization would result in inputs to the soil of ~3-10, 6-8, and 0.5-2 kg $N \cdot ha^{-1} \cdot yr^{-1}$ and gross mineralization would result in inputs to the soil of ~6-10, 7-12, and 0.6-2 kg $N \cdot ha^{-1} \cdot yr^{-1}$ for twigs, roots, and foliage respectively. Species contributions vary by litter type and with respect to net and gross inputs for foliage and roots but for twigs Douglas-fir would contribute the most N and Sitka spruce the least (Table 2.7).

Inputs of N to the soil based on the biomass-disturbance calculations would be greatest for initiation-aged (>12-14 years old) stands in the Coast Range and greatest for mature stands (45-52 years old) in the western Cascades. For Douglas-fir in the Coast Range, the proportion of net N inputs to the soil would be ~64% from foliage,

~12% from roots, and ~24% from twigs and gross inputs would be ~70% from foliage, ~9% from roots, and ~21% from twigs. Most N from Sitka spruce in the Coast Range would be mineralized from foliage for both net and gross inputs to soil, with foliage contributing ~83%, roots contributing ~12%, and twigs contributing ~5% of the net inputs and foliage, roots, and twigs contributing 91%, 9%, and 0%, respectively, of the gross inputs for this species. In the Cascades, foliage would contribute ~ 49%, roots would contribute ~36%, and twigs would contribute ~15% of the net N inputs for bigleaf maple. Gross inputs for bigleaf maple would be ~55% from foliage, ~31% from roots, and ~14% from twigs. Douglas-fir inputs to the soil in the Cascades would be similar for net and gross inputs, ~58% (foliage), ~21% (roots), and 21% (twigs). For total inputs (foliage plus roots plus twigs) to the soil in the Coast Range, N inputs after 2.5 years would be ~13 % (net) and ~16% (gross) greater in a monospecific stand of Sitka spruce than a stand of Douglas-fir. In the Cascades, a stand of Douglas-fir would release ~13-29% (net) and ~6-22% (gross) more N than bigleaf maple. Overall, net N inputs from foliage, roots, and twigs from a disturbance in monospecific stands would range from ~81-151 $kg \cdot ha^{-1}$ in the Coast Range and ~67-168 $kg \cdot ha^{-1}$ in the western Cascades. Gross N inputs in the Coast Range would range from ~109-211 $kg \cdot ha^{-1}$ and from ~88-210 $kg \cdot ha^{-1}$ in the western Cascades (Figures 2.8 and 2.9, Table 2.8). For the biomass estimates used for these calculations see Appendix Table A1.15.

DISCUSSION

The use of ^{15}N-labelled litter in this decomposition study revealed N release patterns that both contrast and agree with findings from other studies. The litter used for this study was fresh and from seedlings. This material had higher N concentrations for a given litter type than other values reported in the literature for either litterfall (e.g. Sollins et al. 1980) or litter used in decomposition studies, many of which used senesced material (e.g. Prescott et al. 2004). Thus, the results from this study may be influenced by the higher N concentrations of the litter used, the fact that litter was fresh, and by the use of litterbags which may result in slower mass loss due to the separation of the decomposing material from the surrounding litter layer or soil (Dornbush et al. 2002).

Influences of site and initial litter chemistry

My results suggest that site environmental differences were likely not large enough to elicit an effect as initial litter chemistry with respect to decomposition and litter N dynamics. Except for mass loss from mesh bags, site played an insignificant role in determining either decomposition rates or N mineralization patterns. This is in accordance with another decomposition study on fine roots at these sites (Chen et al. 2002). Climate is often thought of as an important predictor of decomposition rates, particularly for leaf litter (Meentemeyer 1978, Aerts 1997). In contrast, root litter decomposition does not seem to be as affected by climatic differences but more so by initial root chemistry (Silver and Miya 2001, Chen et al. 2002). Thus, considering the litter used in this study, it could be that the two sites do not differ enough in climatic

attributes (e.g. temperature and precipitation) to produce measurable differences in decomposition or N mineralization or that these attributes are not of primary importance. H. J. Andrews Experimental Forest experiences cooler temperatures and more precipitation in the form of snow, but overall the two sites exhibit similar patterns and values for temperature and monthly precipitation. Mean monthly temperatures for the duration of the study were always less than 10ºC different for the two sites, suggesting that a *Q*10 relationship of a magnitude noticeable to produce differences in decomposition rates was not in effect (Kirschbaum 1995). Additionally, the soil environment could potentially buffer most temperature differences. However, this would only apply to litter decomposed in litterbags that were buried. Still, there was little difference between sites for foliage or twigs decomposing aboveground.

In contrast to site differences, initial litter chemistry was strongly correlated with both decomposition rates and N release. With respect to decomposition, this is in agreement with a large body of literature that describes initial lignin content and/or C:N or lignin:N as key predictors of decomposition rates (Gosz et al. 1973, Staaf and Berg 1982, Melillo et al. 1982, Berg and Ekbohm 1983, Taylor et al. 1989, Aber et al. 1990, Enriquez et al. 1993, Hobbie 1996, Chapin et al. 2002). Twigs had the highest lignin content and the slowest decomposition rate (smallest values for integrated k and k_e), while foliage generally was lowest in lignin and decomposed the fastest, which is what was expected given the established relationship between lignin and decomposition rates.

Initial lignin content was also correlated with N mineralization, however initial N content exhibited even stronger correlations with both net and gross N mineralization. This is consistent with findings from the LIDET study, which determined that global-scale patterns in N immobilization and mineralization for leaf litter were primarily driven by initial N concentrations (Parton et al. 2007). Other studies have also shown initial N concentration to be correlated with N mineralization for both leaf (Berg and Ekbohm 1983, Stohlgren 1988) and root litter (Chen et al. 2002). In contrast to this study and the LIDET results, data from the Canadian Intersite Decomposition Experiment (CIDET) did not indicate a relationship between initial N concentration and N mineralization for multiple species of leaf litter (Prescott et al. 2004). Prescott et al. (2004) suggested that the narrow range of initial N concentrations used in CIDET compared to the LIDET may have constrained their results and thus the ability to distinguish a relationship between initial N and N mineralization. However, for a given litter type, the ranges of initial N concentrations for my study are also comparatively narrow (foliage: 1.00-1.37%, roots: 1.04-1.17%, twigs: 0.62-0.82%). This suggests that the results for my study could be similarly constrained, yet a relationship was still found between initial N concentration and N mineralization. The results for N mineralization from the CIDET study were presented with respect to initial C:N and acid unhydrolyzable residue:N (AUR:N). However, Parton et al. (2007) found that these results were similar to the results from LIDET and my study when presented with respect to litter mass remaining. Given the range of litter types and species used in LIDET, CIDET, and my study it seems

probable that initial N concentration exerts strong control over N release dynamics during decomposition across multiple ecosystems, litter types, and species.

Patterns of N mineralization

All litter types and species mineralized N for the duration of my study and did not exhibit a net N immobilization phase. For leaf litter, these results are in stark contrast to the typical pattern of an N immobilization phase preceding N release (Gosz et al. 1973, Staaf and Berg 1982, Hobbie and Vitousek 2000, Parton et al. 2007). In the global analysis of N mineralization based on the LIDET data, N dynamics for leaf litter were modeled as a function of initial N concentration and litter mass remaining, with N concentrations ranging from < 0.39%-1.98% (Parton et al. 2007). Leaf litters at the higher range of N concentration (1.02% and 1.98%) exhibited very little, if any immobilization but litter at the lower range (<0.395 and 0.58-0.80%) did have a phase of N immobilization before N was mineralized. The initial N concentrations for leaf litter in this study were intermediate between the upper range values for the LIDET study, suggesting that little or no immobilization of N should occur, which is what the results for this study showed.

I applied the same function that was applied to the LIDET data to model N dynamic patterns based on the initial N concentration and PMR data from this study. For all litter types and species, the LIDET model predicted an early net N immobilization phase. For leaf and root litter, the predicted N immobilization phases were smaller in magnitude and of shorter duration than those predicted for twigs, which agrees with the N immobilization patterns observed for data generated by

LIDET study. However, the curves representing the predicted patterns of N dynamics do not fit well with the actual observations of N release for my study. In general the predicted patterns underestimated the amount of N mineralized with respect to both gross and net mineralization. Given that the LIDET model was formulated to model net mineralization, it is logical that the model would underestimate gross N mineralization measured in this study. Additionally, the observed data for leaf litter fall closer to the predicted curves than the observed data for roots or twigs. Since the LIDET model was derived from leaf litter data, it is possible that the model parameters are not appropriate for predicting patterns of N immobilization or release in other litter types despite similarities in initial N concentrations between litter types (e.g., foliage and roots). Another explanation for the differences between the observed and predicted patterns could be that in my study, initial litter concentrations were not exerting as strong a control over N dynamics as compared to the LIDET study.

The decomposition of young, fresh leaf litter (as used in this study) may result in N dynamics that differ from the patterns of N dynamics observed during the decomposition of litter that has undergone senescence and abscission. Due to resorption of nutrients during senescence, abscised leaf litter has lower concentrations of N (and other nutrients) than young, fresh litter. During senescence, approximately half of the N in foliage is resorbed (Aerts 1996, Killingbeck 1996). My study used leaf litter than in essence had double the N concentrations than litter that has undergone senescence used in other decomposition studies. As a result, it would follow that leaf litter used in my study would exhibit different patterns of N dynamics

(e.g. N mineralization with little to no immobilization) than senesced litter relative to initial N concentrations of the litter.

Although this was a comparative study between litter types and species, the results for roots are of particular interest as this is the first study to use ^{15}N to examine N dynamics during fine root decomposition. Up until now, fine root decomposition studies have only examined net N release (Silver and Vogt 1993, Chen et al. 2002, Dornbush et al. 2002, Silver et al. 2005) and the use of ^{15}N has been limited to decomposition studies of leaf litter or lichens (Zeller et al. 2000, Zeller et al. 2001, Holub and Lajtha 2003) or in tracer studies to examine N cycling processes and the fate of N cycling through ecosystems (Preston and Mead 1995, Buchmann et al. 1996, Zeller et al. 2000, Perakis and Hedin 2001, Zeller et al. 2001, Holub and Lajtha 2004). Both the gross and net N mineralization results for roots from this study confirm that decomposing fine roots do exhibit rapid mineralization of N in the early stages of decomposition consistent with patterns observed for net N mineralization from fine roots in both similar and non-similar ecosystems (Silver and Vogt 1993, Chen et al. 2002, Dornbush et al. 2002, Silver et al. 2005). However, because the foliage in this study also exhibited rapid N mineralization without a net N immobilization phase, the results from this study do not completely agree with findings from the LIDET study in which N was mineralized more rapidly from roots than leaf litter (Parton et al. 2007). For bigleaf maple, roots did mineralize N more quickly than foliage, but for Douglas-fir and Sitka spruce, roots mineralized N at a similar rate to foliage or at a slightly slower rate (Sitka spruce and Douglas-fir, respectively). Irrespective of the

differences between leaf and root litter, the N mineralization results from this study support the idea that patterns of N dynamics during fine root decomposition differ from patterns commonly observed in leaf litter.

As for foliage and root litter, twigs showed a mineralization of N throughout the duration of the study. For bigleaf maple and Sitka spruce, mineralization of N from twigs was much slower than N mineralization from foliage and roots of both of these species. However, Douglas-fir twigs exhibited mineralization of N similar to that of foliage and faster than that of roots. Initial lignin and C:N values for Douglas-fir twigs were intermediate between the values for the other two species. In addition, the initial N concentration for Douglas-fir twigs was only slightly higher than that for bigleaf maple twigs and was lower than that for Douglas-fir roots. Thus, Douglas-fir twigs did not follow the patterns of N dynamics expected given the results for the other litter types and species and given the initial chemistry values. One possible explanation for this is that microbial community was preferentially decomposing Douglas-fir twigs as Douglas-fir is the only species of the three that commonly occurs at both study sites. Sitka spruce does not occur in the western Cascades of Oregon, so microbes present at the H. J. Andrews site may be more likely to utilize a substrate that is common to the area. Similarly, at Cascade Head, bigleaf maple is often only a minor component of the forests (Harmon, personal communication) and again the microbial community may preferentially decompose a species that is more abundant. If this was the case, this could potentially result in slower rates of N cycling processes (e.g. mineralization) for bigleaf maple and Sitka spruce twigs as compared to Douglas-

fir twigs. However, this would not explain the more rapid mineralization of N exhibited by Douglas-fir twigs compared to Douglas-fir roots.

N cycling in forested systems

Net N mineralization ranged from 30-87% of gross release in my study. These results are both consistent and inconsistent with findings from other studies examining mineralization in soils. Net N mineralization rates were <14% of gross mineralization rates in forest soils in the western Sierras (Davidson et al. 1992), however in a study spanning a gradient of soil N capital in the Oregon Coast Range, net mineralization ranged from 6-77% of gross mineralization (Sinkhorn 2007). In an incubation study using soil from H. J. Andrews net mineralization was <10% of gross mineralization in the first 50 days of incubation but increased to 20-60% of gross mineralization from 100-456 days (Hart et al. 1994).

A large or increasing percentage of net mineralization as a proportion of gross mineralization indicates that microbial N requirements are being met (Hart et al. 1994, Parton et al. 2007). Considering the percentages of net mineralization relative to gross mineralization for litter in this study, it is possible that microbial communities may not be N-limited at these two sites and were able to meet their N requirements using only litter-N and without immobilizing N from soil N pools. Multiple studies have demonstrated a linear relationship between litter N inputs and net mineralization (Vitousek 1982, Pastor et al. 1984, Reich et al. 1997, Sinkhorn 2007). Thus, it seems plausible given the relatively high initial N concentrations and the initial C:N values of the litter used in my study that net mineralization would be facilitated. With respect to

N content, net N mineralization from leaf litter in the LIDET study was initiated at C:N values ranging from 31-48 (Parton et al. 2007). Foliage and root litter used in my study had C:N values ranging from 35-45 and twigs had values ranging from 57-79. Thus, for leaf and root litter, initial C:N would be expected to facilitate N mineralization whereas twig litter would be expected to show little if any N release. My results are consistent with this trend for foliage and roots for all species; however, only bigleaf maple and Sitka spruce twigs followed this pattern. Again, Douglas-fir twigs were the exception, exhibiting net N mineralization that was 87% of gross mineralization.

With respect to N limitation, there is evidence that the N content of some forest soils in the Oregon Coast Range (including Cascade Head) is high enough to preclude these forests from being N-limited (Perakis et al. 2006, Boyle et al. 2008). Conversely, there is evidence for N-limitation and tight cycling of N in soils at H. J. Andrews (Sollins et al. 1980, Boyle et al. 2008). Estimates of soil N capital ($kg \cdot ha^{-1}$) for this study indicated double the amount of soil N at Cascade Head than H. J. Andrews. When soil N is considered on a per mass basis ($g\ N \cdot kg^{-1}$ soil, values not reported), values are similar to those reported in the literature for these two sites (Hart and Sollins 1998, Boyle et al. 2008). For C:N, values are similar to or slightly lower than other values reported for these two sites (Sollins et al. 1980, Sulzman et al. 2005, Boyle et al. 2008). Given the lack of site differences with respect to N mineralization it seems that differences in soil N capital were not important in determining N release and/or that, given the spatial heterogeneity of soil, plots at H.J. Andrews were not N-

limited enough to facilitate low rates of net N mineralization coupled with high rates of N immobilization.

To examine gross and net N mineralization in an ecosystem framework, I used my data and estimates of litterfall (Grier and Logan 1977) and foliage and root biomass (Campbell et al. 2004) to calculate the potential N inputs to soil in these systems during the early phases of decomposition. With respect to litterfall, I calculated that net mineralization would release ~0.5-2, 6-8, and 3-10 kg $N \cdot ha^{-1} \cdot yr^{-1}$ and gross mineralization would release ~0.6-2, 7-12, and 6-10 kg $N \cdot ha^{-1} \cdot yr^{-1}$ for twigs, roots, and foliage respectively, with species contributions varying by litter type (Table 2.7). For net mineralization, the N inputs to soil from the decomposition of these litter types would range from ~9.5-20 $kg \cdot ha^{-1} \cdot yr^{-1}$and for gross mineralization N inputs to soil would range from ~13.6-24 $kg \cdot ha^{-1} \cdot yr^{-1}$. Atmospheric N deposition to these forested systems is 1.6 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Vanderbilt et al. 2003). Epiphytic N_2-fixation may contribute an additional ~ 5 $kg \cdot ha^{-1} \cdot yr^{-1}$ to forests in the western Cascades (Sollins et al. 1980). The estimated N inputs to soil from net and gross N mineralization from the litter decomposed in this study after one year of decomposition are at a minimum double the annual atmospheric and N_2-fixation inputs. This indicates that decomposing litter exhibiting N mineralization patterns similar to those found in this study may contribute substantial amounts of N to soil in forested systems on an annual basis.

I used the foliage and root biomass estimates from Campbell et al. (2004) to estimate potential N inputs to soil resulting from total mortality of all foliage and root biomass across different age classes for forests in the Coast Range and western

Cascades. This scenario serves as a proxy for a disturbance in a monospecific stand at one point in time in which complete tree mortality occurs but the resulting necromass is left to decompose, such as might occur with windthrow or harvesting where the foliage, branches, and roots may be left on site. Species varied in their relative N inputs, however two patterns emerged from this these estimations due to trends in biomass. For the Coast Range, the greatest N inputs to soil would occur in the in the initiation age class (>12-14 years old). In the western Cascades, the mature age class (45-52 years old) would have the greatest N inputs to soil. Given the relative biomasses for foliage and roots for the various age classes, these patterns in N inputs would be expected. Second, roots would contribute substantially more N in the western Cascades than in the Coast Range (Figures 2.8 and 2.9, Table 2.8).

A third pattern that emerged, though seemingly independent of biomass trends, is the relatively constant ratio of net N inputs to gross N inputs to soil across all ecosystems, litter types, and species within 2.5 years after disturbance. Net N inputs to soil ranged from 72-81% of gross inputs. These values are within the range I reported earlier for net N release as a proportion of gross release (30-87%), although the range resulting from these estimations is much narrower given that the estimations are not weighted by species. If the biomass values were weighted by species, then it seems likely that the narrow range for net N relative to gross N inputs for the disturbance scenario would widen and be more similar to the range reported earlier for my data. Given my data and these estimates, net N inputs to soil from foliage, roots, and twigs within 2.5 years after a disturbance in monospecific stands would range

from ~81-151 kg·ha^{-1} and gross inputs would range from 109-211 kg·ha^{-1} in the Coast Range. In the western Cascades, net N inputs to soil would range from ~67-168 kg·ha^{-1} and gross N inputs would range from ~88-210 kg·ha^{-1}. However, given that a tree consists of more than just foliage or roots, these values clearly underestimate total N inputs to the soil after a disturbance as boles, branches, and will contribute N at some point during the decomposition process. Additionally, given: 1) differences in N release rates in my study (namely between foliage and roots versus twigs), 2) the amount of N remaining in the litter after 2.5 years, and 3) the inclusion of tree boles and branches, it is expected that a temporal component would exist that would influence both the amount of N entering the soil system at any given time and the duration of this release. Such a "cascade" of N release is likely to be over a period longer than the duration of this study.

Conclusions and implications

Multiple global patterns in decomposition-related N dynamics have emerged as the result of large-scale experiments or meta-analyses of multiple data sets. My study confirms these general patterns but also suggests that exceptions to these patterns exist. Namely, I have confirmed that decomposing fine roots do mineralize N even in the earliest phases of decomposition and that initial N concentration is an important factor in determining whether N will be mineralized or immobilized during the decomposition process. I have also demonstrated that net N mineralization may represent a large percentage of gross N mineralization and that this may be similar to

what occurs in some soils. In terms of exceptions, I have shown that it is possible for leaf litter to decompose without exhibiting an N immobilization phase.

This study also demonstrates the potential of decomposing litter to contribute substantial amounts of N to soils in Pacific Northwest forested ecosystems within the first year of decomposition. The true biogeochemical imprint of these inputs and the patterns of N release observed in this study will largely depend upon the fate of this N. This will generally be determined by how tightly N is cycled in these systems. More specifically, N retention mechanisms (e.g. plant uptake or adsorption on to soil particles) and N loss mechanisms (e.g. leaching) will influence the fate of this N. As for decomposition, these mechanisms are regulated by multiple factors interacting at multiple spatial and temporal scales which contribute to the complexity of the N cycle in forested systems. Additional tracer studies highlighting decomposition using ^{15}N-labeled litter could elucidate the spatial and temporal partitioning of N released from decomposing litter. Data with respect to the fate of N, coupled with data such as generated by this study, could then be integrated into models that predict trends in ecosystem attributes and processes such as growth and yield, gross and net primary productivity, decomposition, or carbon dioxide flux.

The world is changing before our eyes as a result of continued and increasing human pressure on the earth's ecosystems. To what extent and how ecosystems will respond to these changes is to some degree unknown, but models have become useful tools for predicting various scenarios of change based on multiple variables related to climate and ecosystem functions. However, for models to provide reliable estimates

with little uncertainty, the model parameters need to be constrained by data generated by studying the fundamental processes at work in ecosystems. Only by understanding the processes themselves can we attempt to understand how such occurrences as disturbance, N deposition, or shifts in community composition may alter the biogeochemical cycling of N and what the potential effects of these alterations may be downstream.

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FIGURES

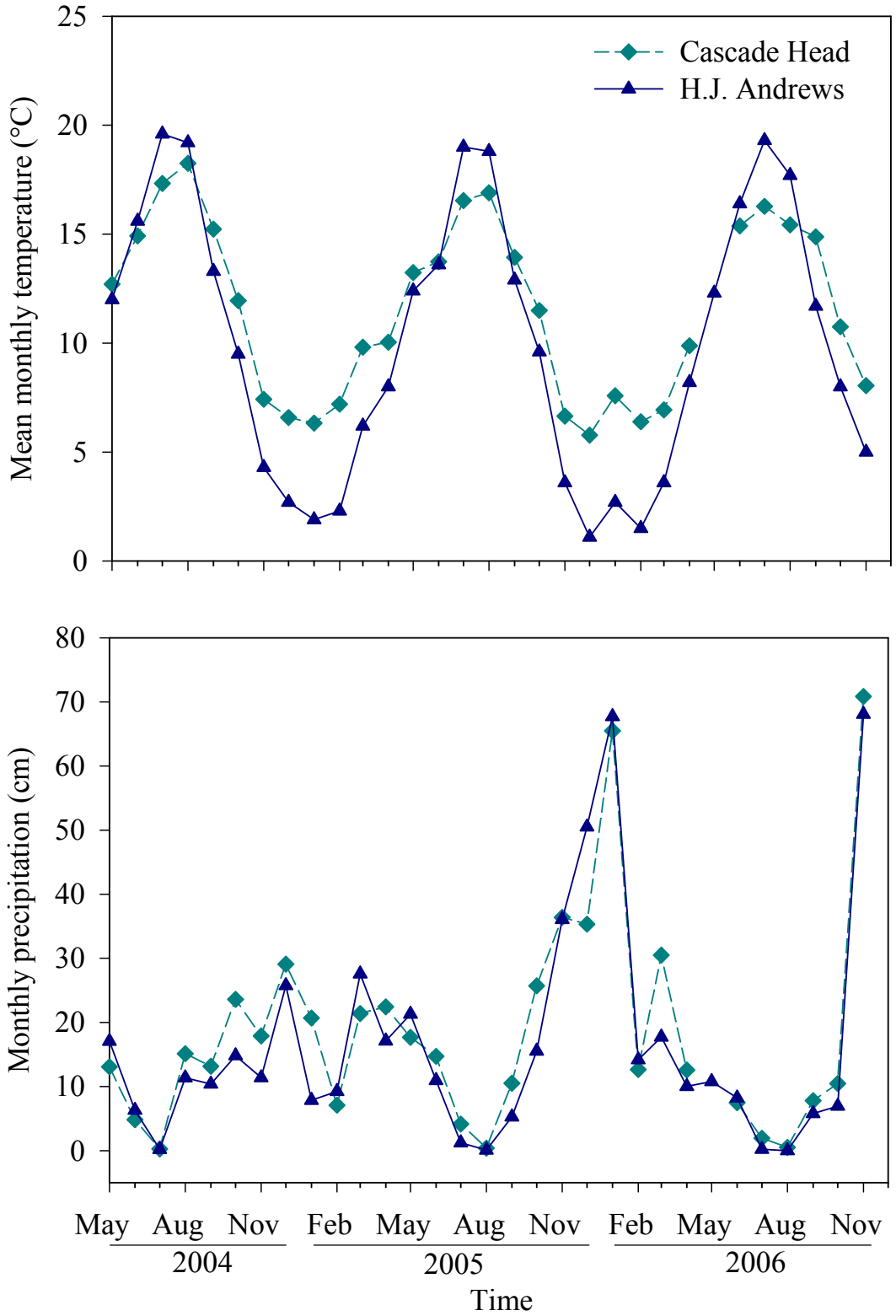

Figure 2.1. Mean monthly temperature and monthly precipitation at Cascade Head Experiment Forest and H.J. Andrews Experimental Forest.

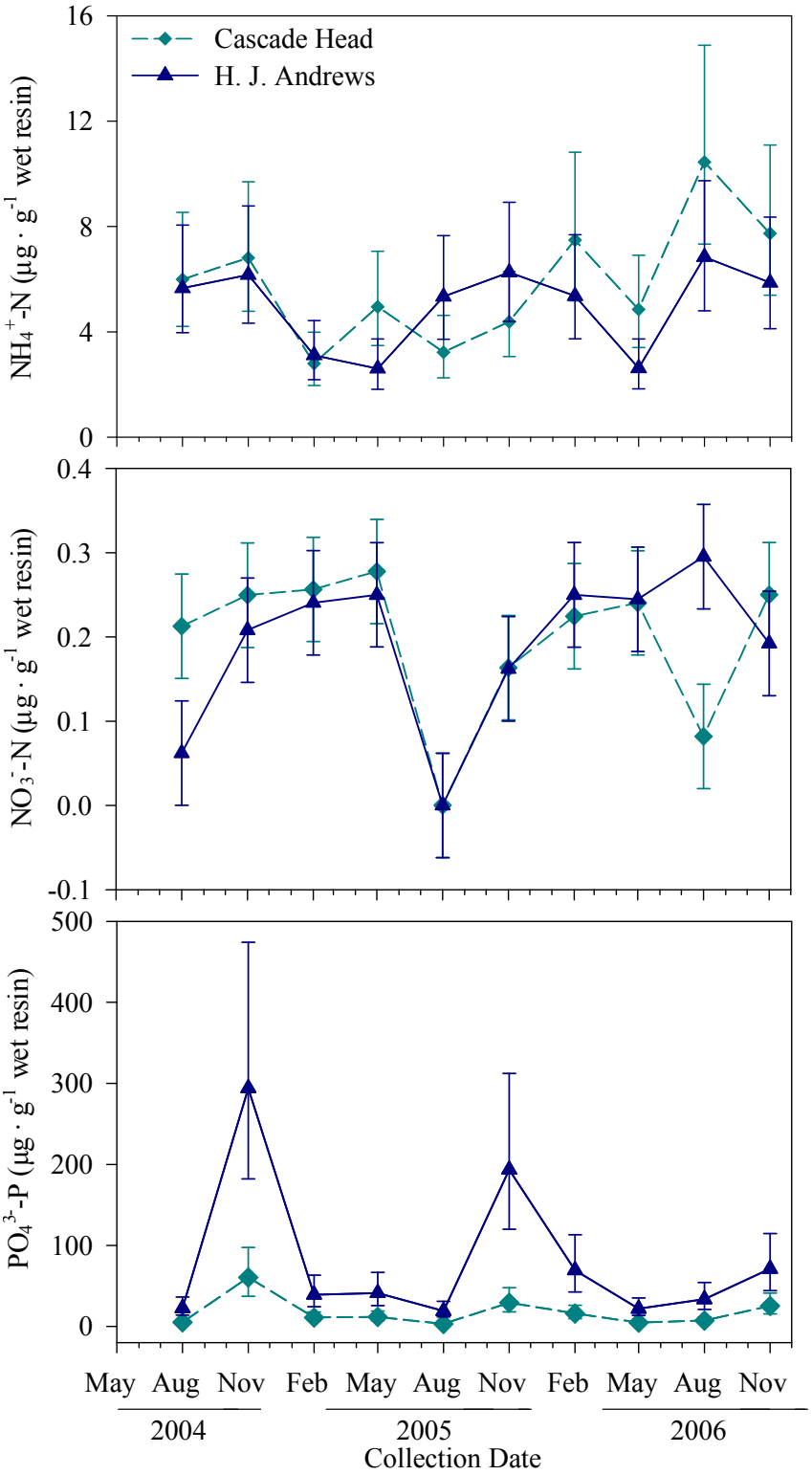

Figure 2.2. Ion exchange resin soil N and P at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest. For NO_3^--N values are means ± 1 SE, n = 6. For NH_4^+-N and PO_4^{3-}-P values are back-transformed means ± 1 SD, n = 6.

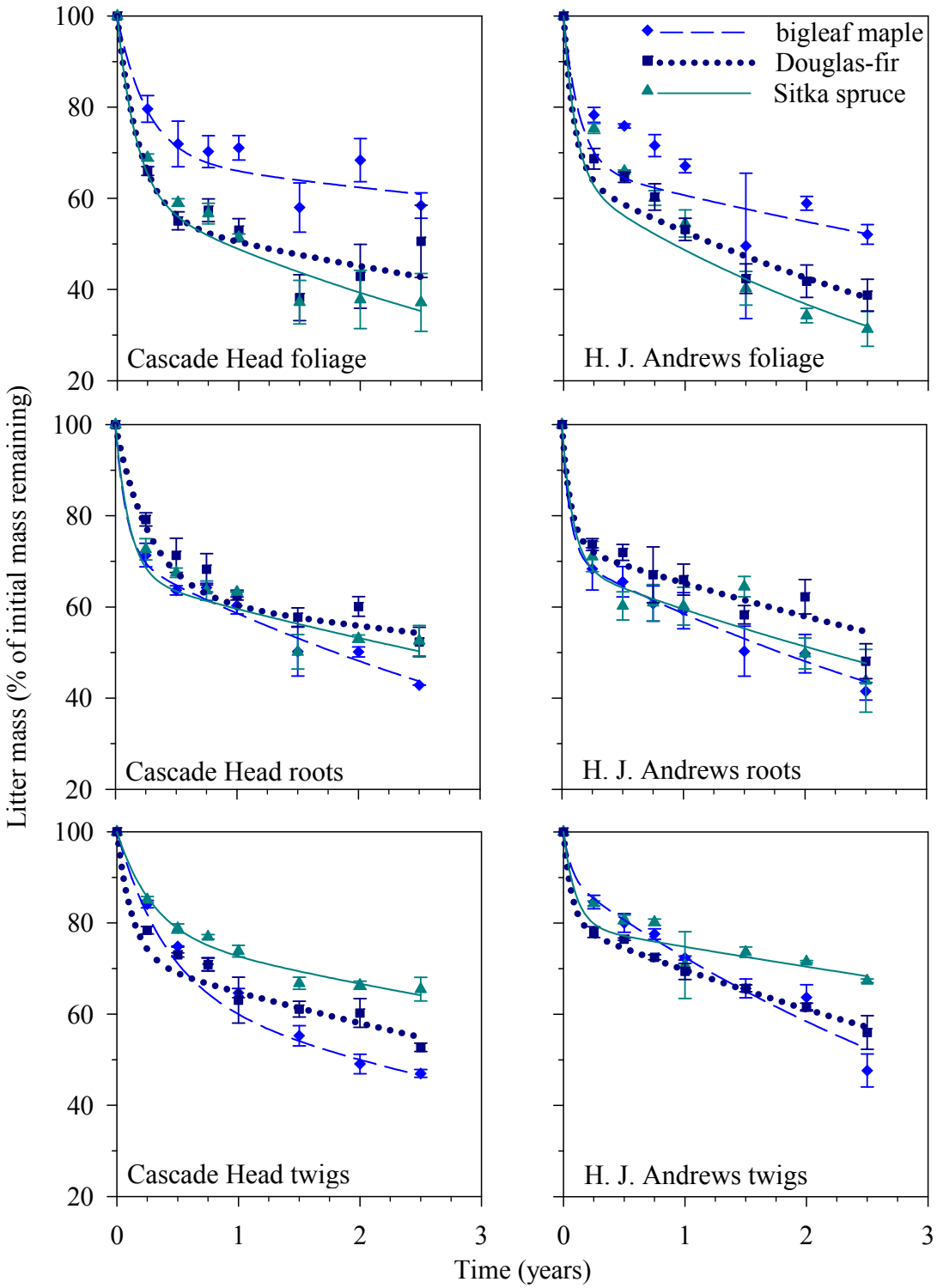

Figure 2.3. Mass loss (as percent of initial mass remaining) of foliage, roots, and twigs from mesh litter bags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest. Values are means ± 1 SE, $n = 3$. Lines are the double-exponential decomposition regression lines based on the coefficients in Table2.3.

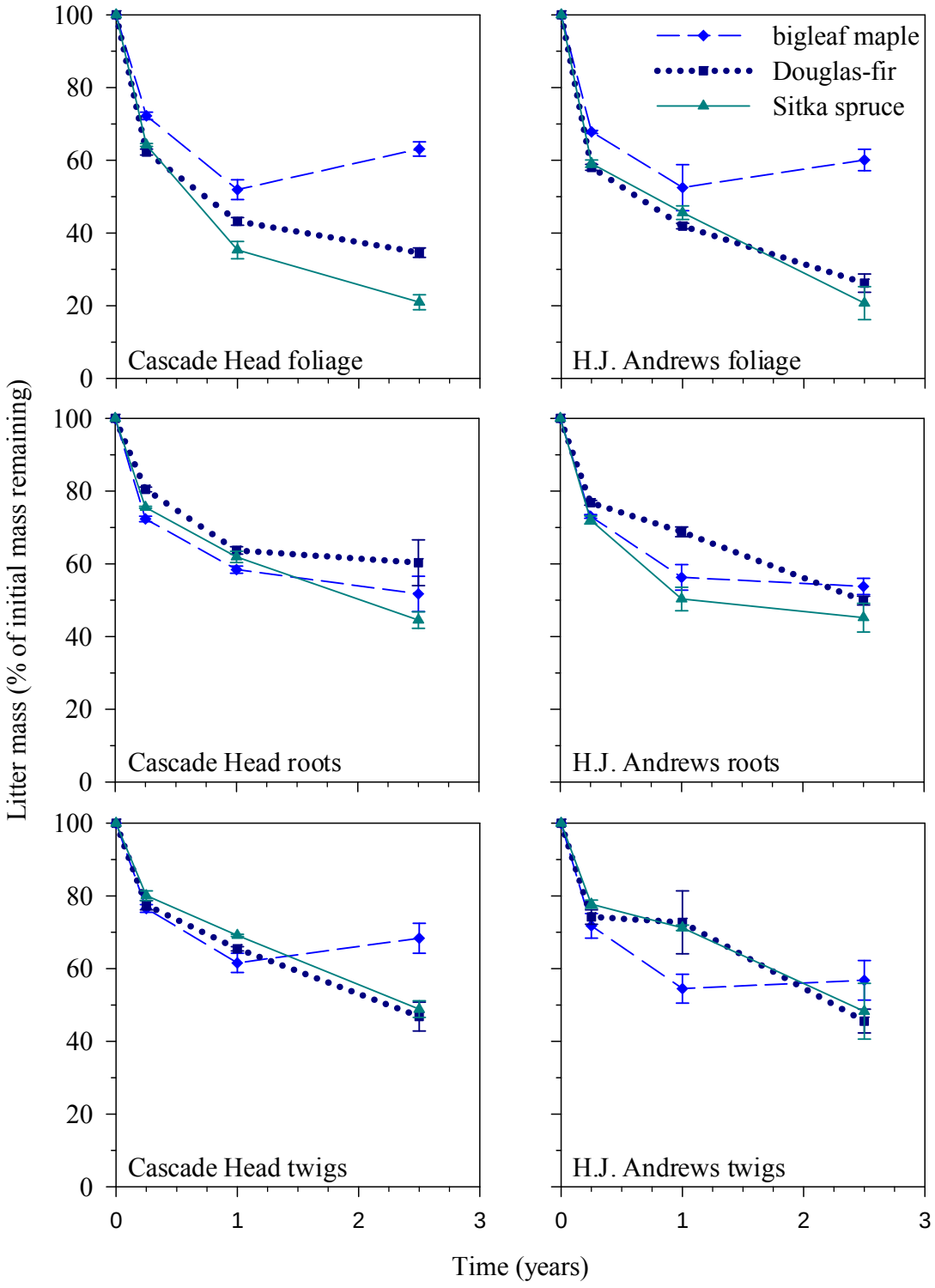

Figure 2.4. Mass loss (as percent of initial mass remaining) of foliage, roots, and twigs from cloth litter bags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest. Values are means ± 1 SE, $n = 3$.

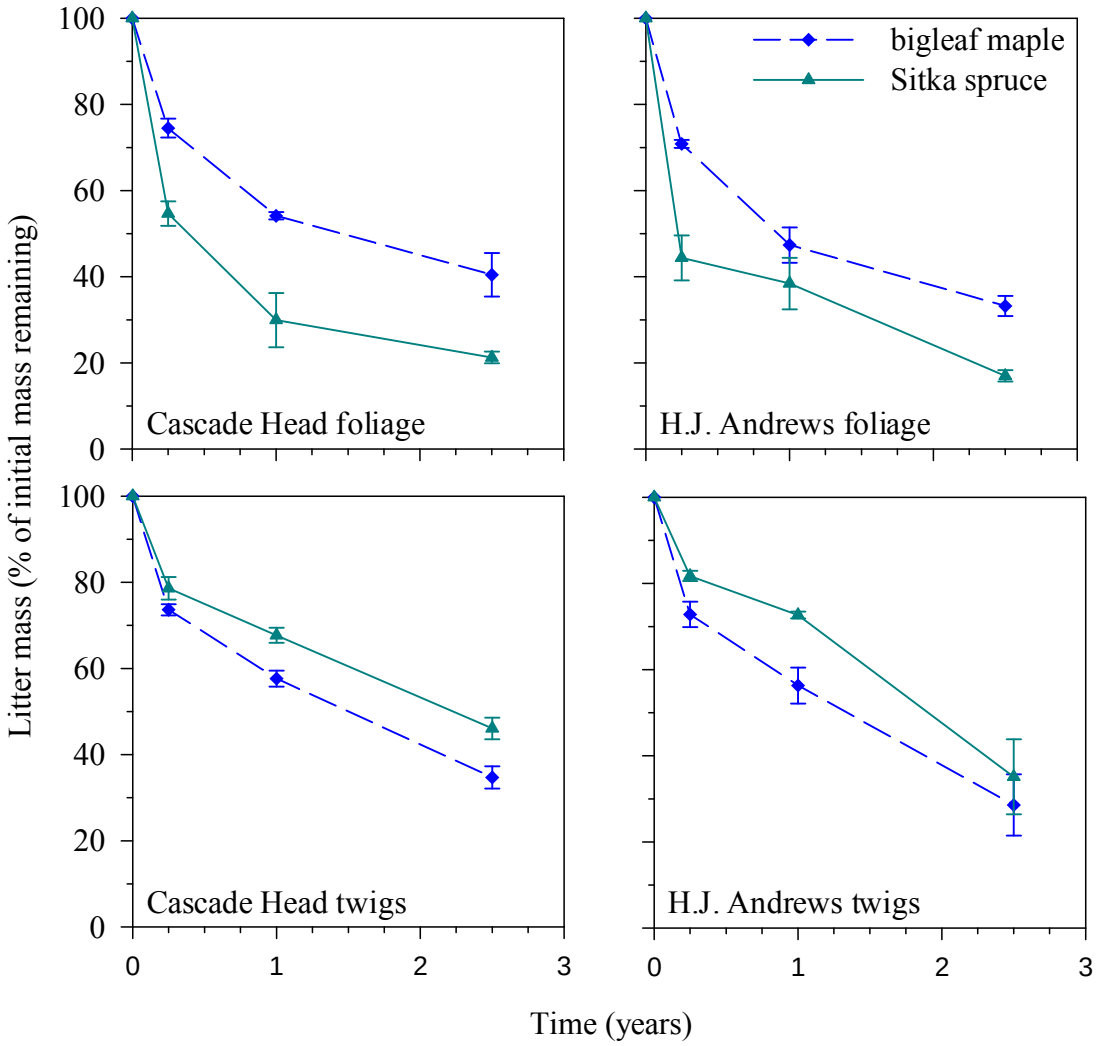

Figure 2.5. Decomposition (as percent of initial mass remaining) of foliage and twigs from additional buried mesh litter bags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest. Values are means ± 1 SE, $n = 3$.

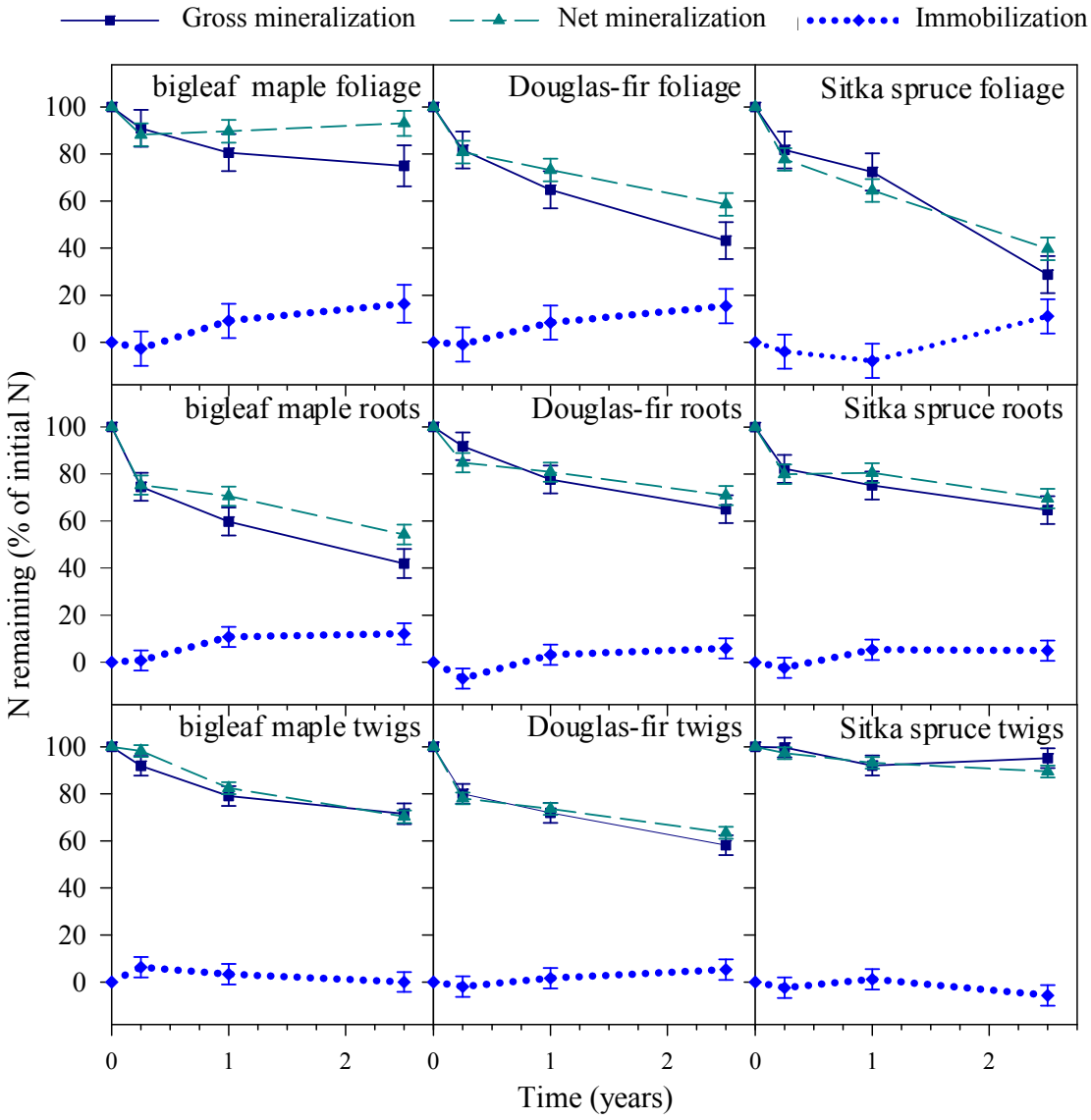

Figure 2.6. N mineralization and immobilization (as percent of initial nitrogen) for litter decomposed at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest. Values are means ± 1 SE, $n = 6$. Values are averaged over site since site was not a significant effect for comparisons of N dynamics.

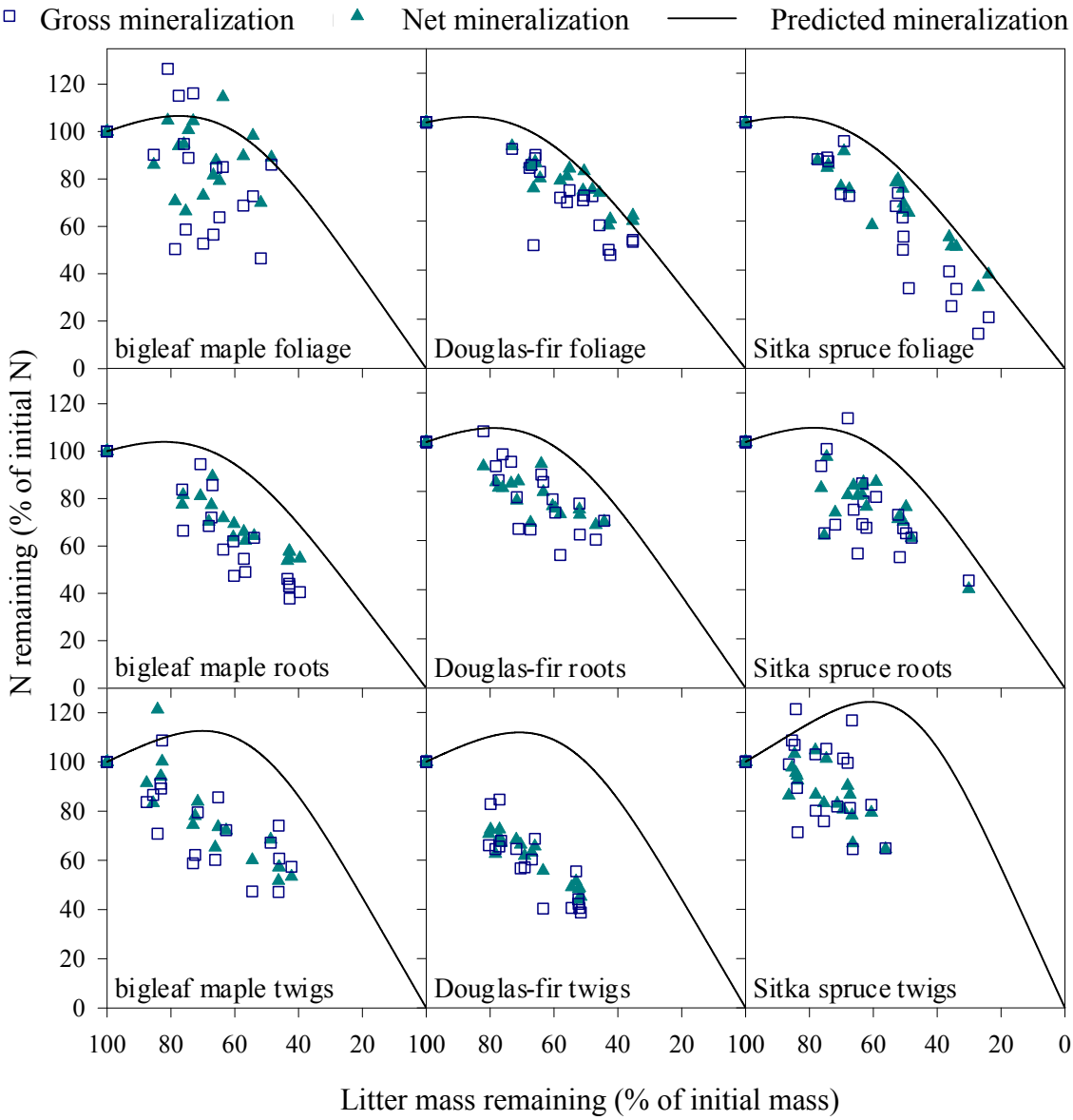

Figure 2.7. Observed gross and net N mineralization (as percent of initial N) versus percent of initial mass remaining for litter decomposed at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest. Lines are predicted N mineralization patterns as a function of initial litter N concentration and mass remaining based on an equation derived from data from the Long-Term Intersite Decomposition Experiment (LIDET) (Parton et al. 2007).

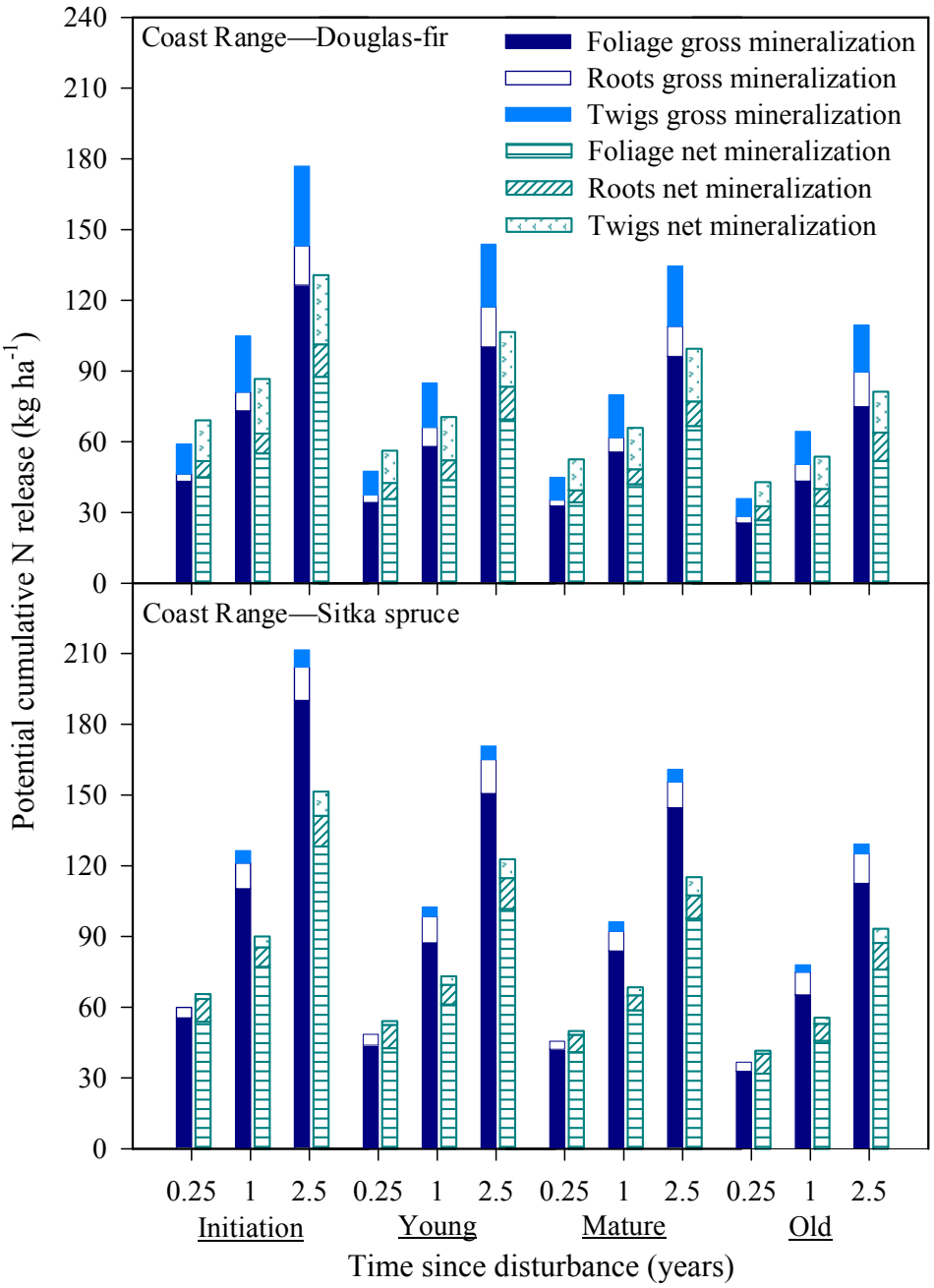

Figure 2.8. Potential cumulative gross and net N mineralization after disturbance in monospecific stands of varying age in the Oregon Coast Range. Net and gross N mineralization amounts were estimated using foliage and root biomass estimates from Campbell et al. 2004. Stand ages are initiation (>12-14 years), young (22-40 years), mature (45-52 years), and old (170-190 years) (Campbell et al. 2004).

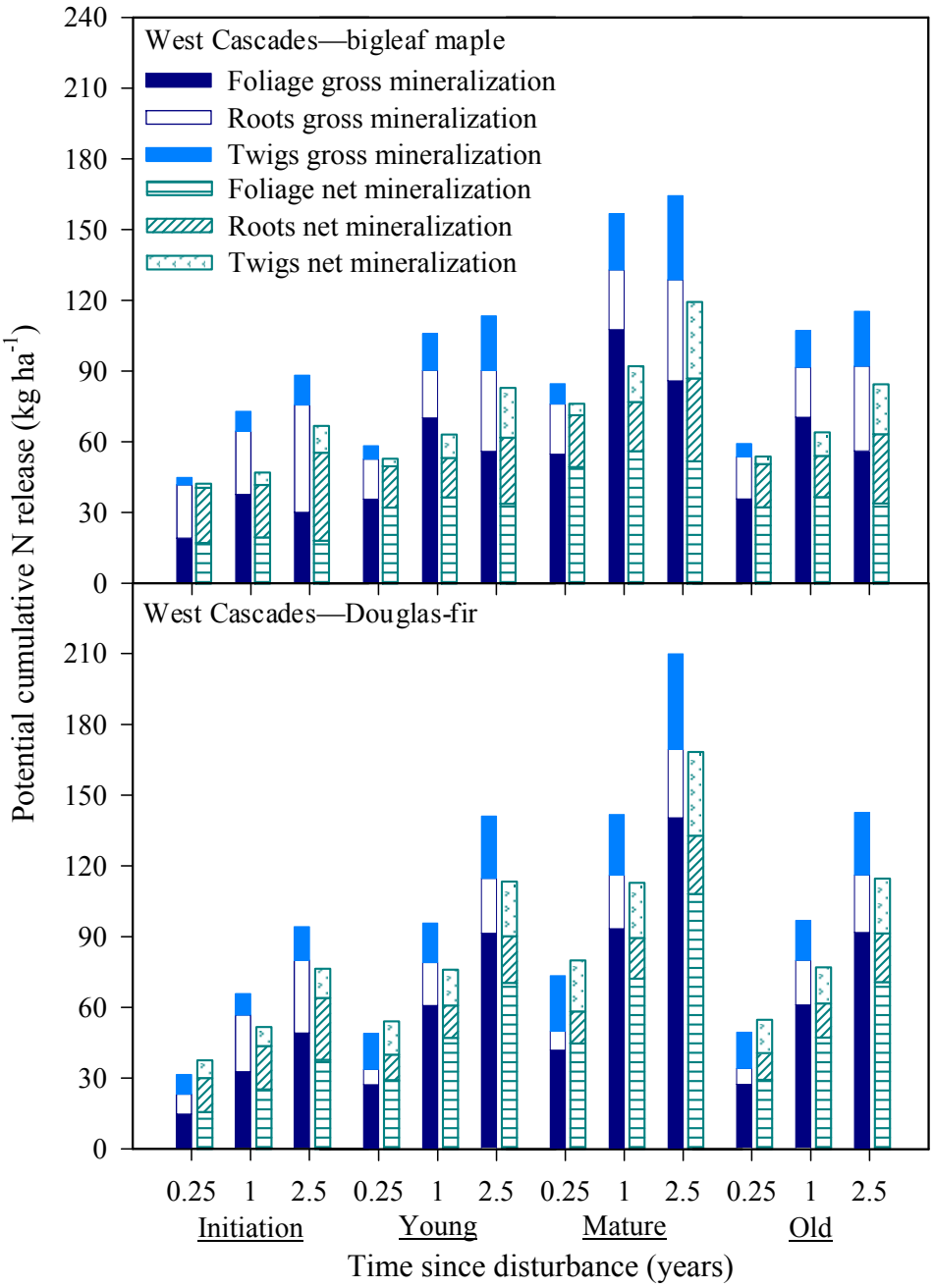

Figure 2.9. Potential cumulative gross and net N mineralization after disturbance in monospecific stands of varying age in the western Cascades of Oregon. Net and gross N mineralization amounts were estimated using foliage and root biomass estimates from Campbell et al. 2004. Stand ages are initiation (>12-14 years), young (22-40 years), mature (45-52 years), and old (170-190 years) (Campbell et al. 2004).

TABLES

Table 2.1. Plot attributes for Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Site	Plot	Latitude (N)	Longitude (W)	Elevation (m)	Soil type
Cascade Head	1	45°03’41”	123°55’60”	274	Andic Dystrudepts†
	2	45°03’43”	123°56’02”	298	Andic Dystrudepts†
	3	45°03’05”	123°54’16”	255	Andic Dystrudepts†
H.J. Andrews	1	44°16’01”	122°10’17”	996	Andisols‡
	2	44°15’20”	122°11’19”	866	Andisols‡
	3	44°13’54”	122°13’33”	561	Andisols‡

† Current soil subgroup classification based on Tillamook County NRCS Soil Survey.
‡ No NRCS soil classification available.

Table 2.2. Mineral soil properties (0-10 cm) for Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Property	Units	Cascade Head	H.J. Andrews
Bulk density	$g \cdot cm^{-3}$	0.320 ± 0.064	0.679 ± 0.049
pH	2:1 H_20:soil	4.35 ± 0.20	5.48 ± 0.12
Soil moisture	%	66.26 ± 3.69	29.44 ± 2.01
DOC*	$kg \cdot ha^{-1}$	501.81 ± 125.48	426.27 ± 134.94
Extractable NH_4^+-N	$kg \cdot ha^{-1}$	5.14 ± 1.82	0.42 ± 0.075
Extractable NO_3^--N	$kg \cdot ha^{-1}$	0.237 ± 0.083	0.033 ± 0.0001
DIN†	$kg \cdot ha^{-1}$	5.38 ± 1.90	0.453 ± 0.075
DON‡	$kg \cdot ha^{-1}$	31.51 ± 9.97	10.70 ± 1.05
TDN^	$kg \cdot ha^{-1}$	36.89 ± 11.63	11.16 ± 1.12
Microbial C	$kg \cdot ha^{-1}$	281.15 ± 65.52	102.29 ± 149.17
Microbial N	$kg \cdot ha^{-1}$	60.91 ± 8.73	38.26 ± 2.67
Microbial C:N	mass:mass	4.88 ± 1.27	2.90 ± 3.85
Total C	$kg \cdot ha^{-1}$	105,128 ± 18,889	57,241 ± 5,460
Total N	$kg \cdot ha^{-1}$	3,824 ± 485	1,865 ± 142
C:N	mass:mass	26.7 ± 1.62	30.6 ± 1.44
Extractable PO_4^{3-}-P	$kg \cdot ha^{-1}$	4.78 ± 1.07	29.99 ± 5.96
Microbial P	$kg \cdot ha^{-1}$	26.31 ± 9.69	12.12 ± 1.30

Notes: Values are means ± SE; $n = 6$.

* Dissolved organic carbon.

† Dissolved inorganic nitrogen (extractable NH_4^+-N + extractable NO^{3-}-N).

‡ Dissolved organic nitrogen.

^ Total dissolved nitrogen (DIN + DON).

Table 2.3. Parameter estimates from the double-exponential regression model used to estimate decomposition (as percent of initial mass remaining) of foliage, roots, and twigs from mesh litterbags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Site	Litter type	Species	Fast fraction (%)	Slow fraction (%)	k_{fast} (yr^{-1})	k_{slow} (yr^{-1})
Cascade Head	Foliage	bigleaf maple	31.39 ± 10.70**	68.61 ± 10.70**	4.05 ± 3.91	0.048 ± 0.095
		Douglas-fir	44.14 ± 10.70**	55.86 ± 10.70**	5.36 ± 3.91	0.107 ± 0.095
		Sitka spruce	39.47 ± 10.70**	60.53 ± 10.70**	6.39 ± 3.91	0.216 ± 0.095*
	Roots	bigleaf maple	28.73 ± 4.64**	71.27 ± 4.64**	11.06 ± 3.57**	0.196 ± 0.036**
		Douglas-fir	37.32 ± 4.64**	62.68 ± 4.64**	3.43 ± 3.57	0.058 ± 0.036
		Sitka spruce	33.30 ± 4.64**	66.70 ± 4.64**	8.70 ± 3.57*	0.113 ± 0.036**
	Twigs	bigleaf maple	34.92 ± 5.77**	65.08 ± 5.77**	2.43 ± 3.06	0.135 ± 0.036**
		Douglas-fir	27.72 ± 5.77**	72.28 ± 5.77**	7.83 ± 3.06*	0.110 ± 0.036**
		Sitka spruce	22.26 ± 5.77**	77.74 ± 5.77**	3.44 ± 3.06	0.077 ± 0.036*
H.J. Andrews	Foliage	bigleaf maple	33.03 ± 10.70**	66.97 ± 10.70**	7.61 ± 3.91	0.100 ± 0.095
		Douglas-fir	34.94 ± 10.70**	65.06 ± 10.70**	11.36 ± 3.91**	0.213 ± 0.095*
		Sitka spruce	35.68 ± 10.70**	64.32 ± 10.70**	10.18 ± 3.91*	0.280 ± 0.095**
	Roots	bigleaf maple	28.76 ± 4.64**	71.24 ± 4.64**	15.40 ± 3.57**	0.197 ± 0.036**
		Douglas-fir	26.51 ± 4.64**	73.49 ± 4.64**	13.67 ± 3.57**	0.119 ± 0.036**
		Sitka spruce	31.00 ± 4.64**	69.00 ± 4.64**	11.29 ± 3.57**	0.148 ± 0.036**
	Twigs	bigleaf maple	10.23 ± 5.77	89.77 ± 5.77**	14.90 ± 3.06**	0.215 ± 0.036**
		Douglas-fir	20.48 ± 5.77**	79.52 ± 5.77**	14.50 ± 3.06**	0.132 ± 0.036**
		Sitka spruce	20.58 ± 5.77**	79.42 ± 5.77**	10.10 ± 3.06**	0.060 ± 0.036

Notes: The regression model used was $PMR = F_{slow}e\text{-}k_{slow}t + (100 - F_{slow})e\text{-}k_{fast}t$ where F_{slow} is the slowly decomposing litter fraction, k_{slow} (yr^{-1}) is the decomposition rate of the slow fraction, k_{fast} (yr^{-1}) is the decomposition rate of the fast fraction, and t is time (years). The fast fraction is equivalent to the model term $100\text{-}F_{slow}$. Values are means ± SE; $n = 3$.
* $P < 0.05$; ** $P < 0.01$.

Table 2.4. Decomposition rate constants (integrated *k* values and k_e values) for foliage, roots, and twigs from mesh litterbags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Site	Litter type	Species	Integrated *k* (yr^{-1})†	Monte Carlo simulation integrated *k* (yr^{-1})‡	k_e (yr^{-1})†
Cascade Head	Foliage	bigleaf maple	0.068 ± 0.121	0.071 ± 0.034	0.321 ± 0.038**
		Douglas-fir	0.183 ± 0.121	0.186 ± 0.182	0.599 ± 0.038**
		Sitka spruce	0.303 ± 0.121*	0.372 ± 0.815	0.640 ± 0.038**
	Roots	bigleaf maple	0.272 ± 0.044**	0.273 ± 0.084	0.479 ± 0.033**
		Douglas-fir	0.084 ± 0.044	0.089 ± 0.256	0.373 ± 0.033**
		Sitka spruce	0.162 ± 0.044**	0.186 ± 1.743	0.438 ± 0.033**
	Twigs	bigleaf maple	0.173 ± 0.043**	0.216 ± 1.109	0.399 ± 0.015**
		Douglas-fir	0.144 ± 0.043**	0.156 ± 0.113	0.357 ± 0.015**
		Sitka spruce	0.097 ± 0.043*	0.098 ± 0.035	0.263 ± 0.015**
H.J. Andrews	Foliage	bigleaf maple	0.131 ± 0.121	0.157 ± 0.424	0.383 ± 0.038**
		Douglas-fir	0.281 ± 0.121*	0.339 ± 2.127	0.575 ± 0.038**
		Sitka spruce	0.341 ± 0.121**	1.017 ± 37.574	0.610 ± 0.038**
	Roots	bigleaf maple	0.275 ± 0.044**	0.278 ± 0.041	0.553 ± 0.033**
		Douglas-fir	0.150 ± 0.044**	0.162 ± 0.152	0.438 ± 0.033**
		Sitka spruce	0.213 ± 0.044**	0.212 ± 0.046	0.443 ± 0.033**
	Twigs	bigleaf maple	0.239 ± 0.043**	0.239 ± 0.040	0.294 ± 0.015**
		Douglas-fir	0.163 ± 0.043**	0.167 ± 0.071	0.317 ± 0.015**
		Sitka spruce	0.071 ± 0.043	0.077 ± 0.070	0.231 ± 0.015**

† Values are means ± SE; $n = 3$.

‡ Values are means ± SD; $n = 10{,}000$.

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

Table 2.5. Initial litter chemistry.

Litter type	Species	Lignin (%)	C ($mg \cdot g^{-1}$ litter)	N ($mg \cdot g^{-1}$ litter)	C:N (mass:mass)
Foliage	bigleaf maple	21.31 ± 0.585	435.15 ± 0.485	10.01 ± 0.474	43.56 ± 2.12
	Douglas-fir	20.28 ± 1.29	491.67 ± 0.88	13.58 ± 0.3465	36.24 ± 0.99
	Sitka spruce	17.34 ± 0.345	482.97 ± 0.69	13.69 ± 0.581	35.35 ± 1.555
Roots	bigleaf maple	26.13 ± 0.755	468.55 ± 3.37	11.67 ± 0.699	40.31 ± 2.70
	Douglas-fir	35.18 ± 1.165	456.01 ± 14.37	10.46 ± 0.2355	43.67 ± 2.36
	Sitka spruce	29.23 ± 0.485	464.72 ± 0.165	10.39 ± 0.9485	45.09 ± 4.13
Twigs	bigleaf maple	10.96 ± 0.89	461.41 ± 0.46	8.06 ± 0.3845	57.41 ± 2.8
	Douglas-fir	23.19 ± 0.64	484.54 ± 0.35	8.22 ± 0.8085	59.51 ± 5.805
	Sitka spruce	25.82 ± 0.06	491.62 ± 2.475	6.22 ± 0.001	79.05 ± 0.39

Notes: Values are means ± SE; $n = 2$.

Table 2.6. N mineralization and immobilization after 2.5 years of litter decomposition in mesh litterbags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Litter type	Species	Gross N mineralization (% of initial N)	Net N mineralization (% of initial N)	N immobilization (% of initial N)	P*
Foliage	bigleaf maple	29.02 ± 4.84	8.83 ± 5.04	19.23 ± 2.73	**0.01**
	Douglas-fir	48.93 ± 4.34	35.67 ± 4.57	13.25 ± 2.47	**< 0.01**
	Sitka spruce	72.54 ± 4.34	52.09 ± 4.57	20.45 ± 2.47	**< 0.01**
Roots	bigleaf maple	57.71 ± 3.62	45.02 ± 3.70	13.91 ± 2.61	**< 0.01**
	Douglas-fir	39.64 ± 3.54	33.05 ± 3.58	6.59 ± 2.80	0.07
	Sitka spruce	39.37 ± 3.54	33.87 ± 3.58	5.50 ± 2.80	0.13
Twigs	bigleaf maple	41.29 ± 4.52	42.22 ± 2.57	1.49 ± 4.37	0.82
	Douglas-fir	58.91 ± 4.80	51.50 ± 2.47	7.40 ± 5.07	**0.02**
	Sitka spruce	9.01 ± 4.80	19.64 ± 2.47	-10.63 ± 5.07	0.18

Notes: Values represent the total amount of N mineralized or immobilized for the 2.5-year duration of the study. Thus, net N mineralization values are the total net N mineralization amounts after 2.5 years and N immobilization values are the total amounts of N immobilized over 2.5 years. Values are means ± SE; $n = 6$.

* Results from a single-sample t-test on the difference between gross N mineralization and net N mineralization. Boldface type denotes a significant ($P < 0.05$) difference.

Table 2.7. Estimated N mineralization from litterfall after one year of decomposition.

Litter type	Species	Litterfall rate† (kg C·ha^{-1} · yr^{-1})	Net N mineralization (g N·kg^{-1} C·yr^{-1})	Net N mineralization (kg·ha^{-1}·yr^{-1})	Gross N mineralization (g N·kg^{-1} C·yr^{-1})	Gross N mineralization (kg·ha^{-1}·yr^{-1})
Foliage	bigleaf maple	1150	2.81	3.23	5.26	6.05
	Douglas-fir	1150	6.39	7.34	8.37	9.62
	Sitka spruce	1150	8.70	10.00	6.76	7.78
Roots	bigleaf maple	1150	7.34	8.44	10.02	11.52
	Douglas-fir	1150	4.99	5.74	5.81	6.68
	Sitka spruce	1150	4.86	5.59	6.19	7.12
Twigs	bigleaf maple	335	4.44	1.49	5.28	1.77
	Douglas-fir	335	6.32	2.12	6.71	2.25
	Sitka spruce	335	1.62	0.54	1.88	0.63

† Based on litterfall estimates from Grier and Logan (1977) and assuming a carbon content of 50% for all litter pools; foliage litterfall rate includes conifers and hardwoods.

Notes: Equal litterfall estimates based on litter type were used for all species, rather than weighting the litterfall estimates by species, to observe the differences in N inputs given equal masses of litter inputs per area and per year. Estimates of N mineralization from this study were then applied to the litterfall estimates to calculate the potential amount of N mineralized given these litter inputs.

Table 2.8. Estimated N mineralization from disturbances in monospecific stands.

Site and species	Age class and age (yr)	Years since disturbance	Foliage net (kg N·ha^{-1})	Foliage gross (kg N·ha^{-1})	Roots net (kg N·ha^{-1})	Roots gross (kg N·ha^{-1})	Twigs net (kg N·ha^{-1})	Twigs gross (kg N·ha^{-1})	Total net (kg N·ha^{-1})	Total gross (kg N·ha^{-1})
Coast	Initiation	0.25	45.02	43.16	6.76	3.16	17.26	12.72	69.04	59.03
Douglas-fir	> 12-14	1	55.10	73.12	8.37	8.00	23.10	23.76	86.57	104.88
		2.5	87.60	126.38	13.71	16.81	29.33	33.63	130.64	176.82
	Young	0.25	35.69	34.21	6.83	3.19	13.68	10.08	56.20	47.48
	22-40	1	43.68	57.96	8.45	8.08	18.31	18.84	70.44	84.88
		2.5	69.44	100.19	13.85	16.98	23.26	26.66	106.55	143.83
	Mature	0.25	34.26	32.85	5.13	2.40	13.14	9.68	52.53	44.92
	45-52	1	41.93	55.64	6.35	6.07	17.58	18.08	65.86	79.80
		2.5	66.67	96.18	10.40	12.75	22.32	25.60	99.39	134.53
	Old	0.25	26.66	25.56	5.91	2.76	10.22	7.53	42.80	35.85
	170-190	1	32.64	43.31	7.32	7.00	13.68	14.07	53.63	64.38
		2.5	51.88	74.85	11.99	14.69	17.37	19.92	81.25	109.47
Coast	Initiation	0.25	53.86	55.47	9.69	4.47	2.07	-3.80	65.62	56.14
Sitka spruce	> 12-14	1	77.23	110.22	8.23	11.01	4.53	5.17	89.99	126.40
		2.5	128.26	190.03	12.95	14.26	10.18	7.20	151.39	211.49
	Young	0.25	42.70	43.97	9.78	4.52	1.64	-3.01	54.13	45.48
	22-40	1	61.22	87.37	8.31	11.12	3.59	4.10	73.13	102.59
		2.5	101.68	150.65	13.08	14.40	8.07	5.70	122.83	170.75
	Mature	0.25	40.99	42.21	7.35	3.39	1.58	-2.89	49.92	42.72
	45-52	1	58.77	83.88	6.25	8.35	3.45	3.94	68.47	96.17
		2.5	97.61	144.62	9.82	10.82	7.75	5.48	115.18	160.92
	Old	0.25	31.90	32.85	8.47	3.91	1.23	-2.25	41.60	34.51
	170-190	1	45.74	65.28	7.20	9.63	2.68	3.06	55.62	77.97
		2.5	75.97	112.55	11.32	12.47	6.03	4.26	93.32	129.29

Notes: Estimated N inputs are based on biomass estimates (Campbell et. al 2004, van Huysen, unpublished data) listed in Table A1.15.

Table 2.8. Continued.

Site and species	Age class and age (yr)	Years since disturbance	Foliage net (kg N·ha^{-1})	Foliage gross (kg N·ha^{-1})	Roots net (kg N·ha^{-1})	Roots gross (kg N·ha^{-1})	Twigs net (kg N·ha^{-1})	Twigs gross (kg N·ha^{-1})	Total net (kg N·ha^{-1})	Total gross (kg N·ha^{-1})
West	Initiation	0.25	17.26	19.09	23.36	22.64	1.71	3.02	42.33	44.75
Cascades	> 12-14	1	19.60	37.58	22.19	26.89	5.33	8.35	47.12	72.82
bigleaf maple		2.5	18.12	29.96	37.36	45.67	11.32	12.45	66.80	88.08
	Young	0.25	32.19	35.61	17.56	17.02	3.18	5.64	52.94	58.26
	22-40	1	36.55	70.09	16.68	20.21	9.95	15.58	63.18	105.88
		2.5	33.80	55.89	28.08	34.32	21.12	23.22	83.00	113.43
	Mature	0.25	49.41	54.65	21.97	21.29	4.89	8.65	76.26	84.59
	45-52	1	56.10	107.57	20.86	25.29	15.27	23.91	92.23	156.76
		2.5	51.87	85.78	35.13	42.94	32.41	35.63	119.41	164.35
	Old	0.25	32.33	35.76	18.37	17.80	3.20	5.66	53.89	59.22
	170-190	1	36.70	70.38	17.44	21.14	9.99	15.65	64.14	107.17
		2.5	33.94	56.12	29.37	35.90	21.21	23.31	84.52	115.34
West	Initiation	0.25	15.64	14.65	14.37	8.58	7.57	8.21	37.58	31.44
Cascades	> 12-14	1	25.22	32.64	18.38	24.14	8.14	8.99	51.74	65.78
Douglas-fir		2.5	37.75	49.05	26.28	30.95	12.41	14.16	76.44	94.16
	Young	0.25	29.17	27.32	10.80	6.45	14.12	15.31	54.09	49.08
	22-40	1	47.04	60.89	13.81	18.14	15.18	16.77	76.04	95.80
		2.5	70.41	91.50	19.75	23.26	23.15	26.41	113.32	141.16
	Mature	0.25	44.77	41.93	13.51	8.07	21.68	23.50	79.95	73.50
	45-52	1	72.20	93.45	17.28	22.70	23.30	25.74	112.78	141.88
		2.5	108.07	140.42	24.71	29.10	35.53	40.53	168.31	210.05
	Old	0.25	29.29	27.43	11.29	6.75	14.18	15.38	54.77	49.56
	170-190	1	47.24	61.14	14.45	18.98	15.25	16.84	76.93	96.96
		2.5	70.71	91.88	20.66	24.33	23.25	26.52	114.61	142.72

CHAPTER 3:
EFFECTS OF PHOSPHORUS AVAILABILITY ON DECOMPOSITION DYNAMICS OF MULTIPLE LITTER TYPES IN TEMPERATE CONIFEROUS FORESTS

ABSTRACT

Litter nutrient concentrations and soil nutrient availability may influence decomposition rates and litter nutrient dynamics either independently or synergistically. I assessed whether increased litter phosphorus (P) concentrations and increased soil P availability influenced decomposition rates and litter nutrient dynamics of multiple litter types in nitrogen (N)-rich Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in the Oregon Coast Range. Over the course of 2 years, fresh foliage, fine root, and twig litter from Douglas-fir seedlings was decomposed at three sites. Half of the seedlings and half of the plots at each of the sites were fertilized with P resulting in a factorial design with the following treatments: control (no P fertilization), plant P (P-fertilized litter), soil P (P-fertilized soil), and plant P × soil P. Soil P fertilization resulted in slight decreases in decomposition rates for foliage. Plant fertilization increased litter P concentrations by an average of 250% relative to controls, but did not alter litter decomposition rates. Litter mineralized P rapidly early in the decomposition process compared to N, which was mineralized more slowly with some litter immobilizing N. Litter P concentrations decreased over the 2 years for all treatments, whereas N concentrations increased. Decomposition rates and mineralization of N and P were strongly related to initial litter chemistry. Initial litter element ratios differed due to fertilization of seedlings with P, but over the 2 years element ratios (C:N, C:P, N:P) converged to similar values across treatments within a given litter type. The results of this study suggest that litter

P concentrations and to some extent soil P may influence litter nutrient dynamics during decomposition.

INTRODUCTION

In plants, phosphorus (P) is a key component of sugar phosphates, nucleic acids, coenzymes, and phospholipids. It is also a component of nucleotides that make up ATP, and thus is important for plant metabolism, as well as nucleotides that make up DNA and RNA (Taiz and Zeiger 2002). P differs from carbon (C) and nitrogen (N) in that its primary source is not the atmosphere and its availability in soils is primarily controlled by geochemical, rather than biological reactions (Chapin et al. 2002). The major input of P to ecosystems comes from the weathering of primary minerals, mainly calcium apatite (Walker and Syers 1976, Crews et al. 1995). This weathering releases P which either enters the organic P pool, through uptake by organisms, or is sorbed onto the surface of secondary minerals (Crews et al. 1995). Over millennia, the dissolution of secondary silicate minerals from soils gives way to Al and Fe oxides, which have a strong affinity for P (Brady and Weil 1996, Chapin et al. 2002) . Thus, sorbed P will remain labile for a period of time, but if not taken into the organic P pool will eventually become occluded by Al and Fe hydrous oxides (Uehara and Gillman 1981, Chapin et al. 2002). Ultimately, continued weathering of P-containing primary minerals coupled with increasing concentrations of Al and Fe oxides over time leads to a decline in soil P availability (Walker and Syers 1976, Crews et al. 1995, Chapin et al. 2002). This is characteristic of certain soil orders that are defined as being highly weathered. However, allophane, a clay present in soils derived from volcanic ash, also occludes P and thus decreases P availability in these soils as well (Brady and Weil

1996). P availability is also largely dependent on the pH of soil due to the low solubility of Al-P and Al-Fe complexes at low pHs and the low solubility of calcium phosphate at high pHs in soils with high concentrations of exchangeable calcium (Brady and Weil 1996).

Decomposition is an important ecosystem process due to its influence on nutrient cycling, primary production and carbon storage, soil organic matter formation (Hobbie and Vitousek 2000, Chapin et al. 2002). This process links plants and soils and represents a pathway by which plants and soils feedback to one another (Vitousek 1982). In ecosystems with low soil P-availability, organic P is tightly cycled between plants and organic matter such that this P remains in the organic P pool rather than entering the soil pool where it may complex with other ions or sorb to minerals as described above (Crews et al. 1995, Chapin et al. 2002). However, despite this tight cycling of P, studies have shown that ecosystems with low soil P-availability may still experience P-limitation of above- and belowground net primary productivity as well as decomposition rates (Vitousek and Farrington 1997, Hobbie and Vitousek 2000, Ostertag 2001, Cleveland et al. 2002). Further, some studies suggest that soil P availability may influence litter nutrient dynamics during decomposition (Ostertag and Hobbie 1999, Hobbie and Vitousek 2000, Ostertag 2001, McGroddy et al. 2004b, Cleveland et al. 2006).

Given that plants and soils are inextricably linked, it is important to consider not only the effects soil nutrient availability may have on decomposition rates and nutrient dynamics, but also the potential effects of initial litter nutrient concentrations. However, results regarding the relationship between litter nutrient concentrations and

decomposition rates are mixed (Hobbie and Vitousek 2000, Prescott et al. 2004). Further, there are few studies that have examined the effect of increased litter nutrient concentrations on decomposition rates. In contrast, initial litter nutrient concentrations, particularly N and P, seem to have a strong effect on litter nutrient dynamics (Hobbie and Vitousek 2000, Chen et al. 2002, Parton et al. 2007). Recent evidence suggests that N release from decomposing foliage can be predicted from initial N concentrations (Parton et al. 2007) and that initial litter N:P may predict patterns of P release or immobilization during decomposition (Moore et al. 2006).

I attempted to elucidate whether P availability serves as a proximate control over litter nutrient dynamics during decomposition by manipulating endogenous (litter) and exogenous (soil) P availability. I used a factorial fertilization and decomposition time series study in N-rich Douglas-fir forests in the Oregon Coast Range to examine whether increasing P availability in soils and/or increasing initial litter P concentrations influence decomposition rates and litter N and P dynamics of multiple litter types. Further, by shifting initial litter N:P stoichiometry, this study provides insight into the importance of multiple-element versus single-element influences on decomposition.

METHODS

Site description

I conducted this research in the Oregon Coast Range at three plantations owned by Green Diamond Resource Company, Tillamook, OR, USA. Sites were chosen based on data indicating low extractable P, high foliage N:P, and having soils derived from sandstone (Perakis et al. 2006) . Site 5 (44º38’ N, 123º48’ W) is ~16 km

inland from the Pacific Ocean, close to the town of Eddyville at an elevation of 322 m. The mean annual precipitation at this site is 1730 mm and the mean annual temperature is 11.2ºC. Soils are fine-loamy, isotic, mesic Andic Dystrudepts of the Preacher-Bohannon-Slickrock complex. Slopes are 55% and the aspect is 220º. Site 39 (45º44' N, 123º53' W) is ~4.5 km inland from the coast near the town of Nehalem. Elevation at this site is 23 m, slopes are 10%, and the aspect is 160º. The mean annual precipitation at site 39 is 2000 mm and the mean annual temperature is 10.3ºC. Soils at this site are fine-silty, isotic, isomesic Andic Dystrudepts of the Templeton and Ecola series. Site 58 (44º43' N, 123º49' W) is ~20 km inland from the coast near the town of Siletz at an elevation of 80 m. The mean annual precipitation is 1750 mm and the mean annual temperature is 10.8ºC. Soils are fine-loamy, isotic, mesic Andic Dystrudepts of the Preacher-Bohannon-Slickrock complex. Slopes are 15% and the aspect is 75º. The plantations are 24-30 yrs old, and sites 5 and 58 were burned prior to being planted. At each site, 3 plots were established which were then divided into 4 subplots, half of which were fertilized by hand with 800 $kg \cdot ha^{-1}$ triple superphosphate (equivalent to ~200 $kg \cdot ha^{-1}$ P) in January 2005.

Soil Chemistry

The mineral soil was sampled 5 times over the course of 2 years, concurrent with collection of litterbags (see below). After removal of surface litter, two soil cores were collected randomly to a depth of 10 cm from each treatment plot using a 6.7 cm diameter steel corer. Cores from each plot were composited in a polyethylene bag and kept on ice for transport bag to the lab. Prior to analysis, composited samples were sieved to 2 mm. The < 2 mm fraction was used for all subsequent soil analyses.

Gravimetric soil moisture content was determined by drying a 10 g subsample of soil for 48 h at 105°C. Soil solution pH was determined in a 2:1 ratio of deionized water:field-moist soil. The soil water solution was allowed to equilibrate for 30 min after which the pH of the supernatant was measured using an Accumet pH meter with a glass-body combination probe (Fisher Scientific, Hampton, NH, USA).

Extractable P was determined by acid-fluoride extraction (Bray and Kurtz 1945). Twenty-five mL of extractant (NH_4F-HCl) was added to a 5 g subsample of field-moist soil in a centrifuge tube. Samples were shaken by hand for 1 min and then centrifuged for 5 min at 3400 rpm (IEC multi centrifuge, Thermo Electron Corporation, Milford, MA, USA). The supernatant was then filtered through Whatman 42 filter paper in funnels. Filtrates were collected in 20 mL polyethylene scintillation vials. Extracts were analyzed immediately or frozen until analysis using the molybdate blue colorimetric method for ortho-phosphate (PO_4^{3-}-P) (QuikChem Method 12-115-01-1-A, Lachat Instruments, Milwaukee, WI, USA). To determine chloroform-labile P ($CHCl_3$-P), a second set of soil subsamples was fumigated with chloroform using the chloroform-direct-extraction method (Davidson et al. 1989). Soil samples were placed in a dessicator lined with wet paper towels along with a flask of ~50 mL chloroform. The dessicator was evacuated 3 times, allowing the chloroform to boil for 2 min on the first evacuation. At the end of the 3rd evacuation, the dessicator was sealed. Samples were incubated in the dark at room temperature (~25°C) for 24 h, allowed to vent to the atmosphere for 10 min, and then extracted and analyzed as above for PO_4^{3-}-P.

Extractable NH_4^+, NO_3^- , total dissolved N (TDN) and total C (TC) were determined in a 7 g subsample of field-moist soil extracted with 35 mL of 0.5M K_2SO_4 in snap-cap vials. After the addition of K_2SO_4, samples were shaken for 1 h, allowed to settle for 30 min, and then filtered through pre-rinsed Whatman 42 filter paper in funnels. Filtrates were collected in 20 mL polyethylene scintillation vials. Extracts were analyzed immediately or frozen until analysis. Extracts were analyzed for NH_4^+ colorimetrically using the salicylate method (QuikChem Method 12-107-06-2-E, Lachat Instruments, Milwaukee, WI, USA). Extracts were analyzed colorimetrically for NO_3^- using the cadmium reduction method (QuikChem Method 12-107-04-1-H, Lachat Instruments, Milwaukee, WI, USA). Extracts were analyzed for dissolved organic carbon (DOC) and total dissolved N (TDN) by catalytic oxidation combustion using a Shimadzu TOC-V CSH total organic carbon analyzer with a TNM-1 total nitrogen measuring unit (Shimadzu Scientific Instruments, Columbia, MD, USA). To determine $CHCl_3$-C and $CHCl_3$-N, a second set of soil subsamples was fumigated with chloroform as above. Fumigated samples were extracted and analyzed as above for NH_4^+ (QuikChem Method, Lachat), NO_3^- (QuikChem Method, Lachat), and TN and TC. Blanks were collected for all soil extractions using the same methods as used for the soil samples. For blanks, no soil was added to the containers used for extractions. Blanks were analyzed as above with the corresponding soil extracts. For total C and N, approximately 20 g subsamples of field-moist soil were dried at 65°C for 72 h and ground to a powder on a roller mill (~2 h). Samples were analyzed for C and N on a Costech ECS-4010 elemental

combustion analyzer (Costech Analytical, Valencia, California, USA) using an Atropine standard.

Decomposition and litter chemistry

Litter was obtained from two-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings planted in 1-gallon pots of peat moss and maintained in an open-air greenhouse from May-October 2004. Half of the seedlings were fertilized with 2.3 g triple superphosphate-P per pot in August, September, and October 2004. Seedlings were harvested in November 2004 and allowed to air dry. Once dry, seedlings were separated into foliage, roots, and twigs, and composited within treatments (control and fertilized). Litter bags constructed of 1-mm nylon mesh were filled with 3.5 g samples of either root or twig samples from each species. For foliage, 3.5 g samples were placed in litter bags with 1-mm nylon mesh tops and 55 μm Dacron mesh bottoms. Subsamples of initial litter from the seedlings were retained to analyze for moisture content, lignin, and total C, N, and P.

I placed litter bags in the field in February 2005 and allowed them to decompose over a two year period. To assess the influence of exogenous P supply on both decomposition and litter nutrient (i.e., N and P) dynamics, litterbags with control and P-fertilized litter were placed in P-fertilized and un-fertilized subplots at each site. The resulting factorial experiment had three treatments and a control to contrast decomposition between differing endogenous and exogenous P supplies. Litter bags containing root samples were buried at a depth of 10 cm. Subsets of litterbags (one litterbag per litter type per treatment per plot per site) were collected over two years, with collections in May 2005, August 2005, February 2006, August 2006, and

February 2007. Litterbags were kept on ice for transport back to the lab. After collection, litter samples were dried at 65°C until samples reached a constant mass and then weighed. Dried litter was ground on a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA), ground on a roller mill to a powder, and then stored in 20 mL scintillation vials. Prior to analysis, samples were dried again for 24 h at 65°C and then placed in a dessicator. To determine ash-free dry mass (AFDM), 1 g subsamples of dried litter were ashed in a muffle furnace for 4 h at 500ºC. Lignin content of initial samples was assayed using the acid detergent method at the University of Nebraska-Lincoln Soil and Plant Analytical Laboratory (Lincoln, NE, USA). Dried and ground litter subsamples were weighed into tin capsules and analyzed for total C and N against an Atropine standard as described above for soil samples.

To assay litter P content, dried and ground 0.5 g litter subsamples were weighed into ceramic crucibles and ashed for 12 h at 475°C in a muffle furnace. After the samples cooled, 5 mL of 5M HCl was added to each crucible and swirled to remove any ash on the sides of the crucibles. Each sample was then diluted with 5 mL of deionized water and filtered through pre-rinsed Whatman 42 filter paper in a funnel, followed by four subsequent 10 mL crucible rinses with deionized water. Filtrates were collected in 50 mL polyethylene bottles and refrigerated at 4°C until analysis. Filtrates were analyzed for total P colorimetrically using the molybdate blue method for PO_4^{3-}-P (QuikChem Method 10-115-01-1-O, Lachat Instruments, Milwaukee, WI, USA). Volumes of acid and deionized water were adjusted for samples that had less than 0.5 g available for digestion.

Calculations and statistical analyses

Dissolved inorganic N (DIN) was calculated as the sum of NH_4^+ and NO_3^-. Dissolved organic N (DON) was calculated TDN minus DIN. Chloroform-labile microbial C, N, and P were calculated as fumigated TC, TN, and inorganic P minus corresponding values measured in unfumigated samples. Values were corrected by subtracting extraction blank values

The statistical software package SAS 9.1 (SAS Institute, Cary, NC, USA) was used for all analyses. Prior to analysis, normal probability plots were used to check data distributions for normality and residual plots were used to check for homogeneity of variances. Log transformations were applied when necessary. Results were considered significant at $P < 0.05$.

Soil chemistry variables were compared with Analysis of variance (ANOVA) using a mixed effects model with repeated measures (PROC MIXED in SAS 9.1). Fixed effects were site, plant P, soil P, and time and all interactions. The random effects were plot (site), where site is nested within plot, and site × plot × plant P × soil P. The subject of the repeated measures was site × plot × plant P × soil P × time.

Mass loss is expressed as percent of initial litter mass remaining for all litter types and was calculated using ash-corrected litter mass values:

(1) $$PMR = (M_t / M_i)*100$$

where PMR is percent of initial mass remaining, M_t is litter mass for a given collection time, and M_i is initial litter mass. An ANOVA mixed effects model with repeated measures (PROC MIXED in SAS 9.1) was used to compare PMR. Fixed effects were site, plant P, soil P, litter type, and time and all interactions. The random effects were

plot (site), where site is nested within plot, and site × plot × plant P × soil P. The subject of the repeated measures was site × plot × plant P × soil P × litter type × time. To calculate decomposition rates, PMR data was converted to proportion of mass remaining by dividing by 100 (e.g. PMR of 100 equals proportion of mass remaining of 1). The proportion of mass remaining data was transformed to the natural logarithmic scale resulting in a value of zero for the initial mass on the log scale. This value of zero represents the y-intercept. Linear regression (PROC REG in SAS 9.1) was then used to test whether the intercepts for regression lines fitted to the log-transformed proportion data were significantly different from zero. This test was used to determine whether linear or non-linear regression was appropriate for analyzing the PMR data and calculating decomposition rate constants. If the intercept of the regression line was significantly different from zero ($P<0.05$), this indicated that non-linear regression was appropriate to describe mass loss dynamics. However, due to only five collection time points, there was insufficient data to run a non-linear analysis using a double-exponential decomposition model to obtain *k* values for fast and slow litter pools as in Chapter 2. Instead, a calculation was used to estimate what I term "single exponential equivalent *k*" values (k_e). The calculation, based on numerical approximation, keeps a running total of the area under the decomposition curve and then derives the k_e value for each site × plot × litter type × treatment combination that would result in this calculated area if decomposition did follow a negative single exponential curve. The total area under the curve is the sum of rectangular divisions that correspond to PMR data (expressed as proportion of mass remaining) for given times and the k_e value is then estimated as the inverse of the total area. The k_e values

are not steady-state decomposition rates as they only represent the rates for 2 years of decomposition. Values for k_e were compared using a mixed effects model with repeated measures (PROC MIXED in SAS 9.1). Fixed effects were site, litter type, plant P, soil P, and all interactions. The random effects were plot (site), where site is nested within plot, and site × plot × plant P × soil P. The subject of the repeated measures was site × plot × plant P × soil P.

Initial litter C, N, P, C:N, C:P, and N:P were analyzed statistically using separate two-way ANOVAs with litter and treatment as main effects and including the litter type × treatment interaction (PROC GLM in SAS 9.1). A Tukey adjustment was used for multiple comparisons. Loss of C, N and P from decomposing litter was calculated as the difference between initial litter C, N or P content and the C, N or P content of litter samples collected at a given time and represents C release and net N or P release. Litter C and N content of decomposing samples and C and net N and P release were compared using a mixed effects model with repeated measures. Fixed effects were site, plant P, soil P, and litter type and all interactions. The random effects were plot (site), where site is nested within plot, and site × plot × plant P × soil P. The subject of the repeated measures was site × plot × plant P × soil P × litter type. Litter P content of decomposing samples was compared using a similar model but with the removal of plant P as an effect. I explored the relationships between initial N concentration and net N release by applying equations used to model patterns of N release during leaf litter decomposition in the Long-Term Intersite Decomposition Experiment (LIDET) to my data (Parton et al. 2007). Relationships between initial

litter chemistry (element concentrations and ratios), k_e values, and N and P release were explored using Pearson correlation coefficients.

RESULTS

Soil chemistry

Of all the soil pool variables, P fertilization treatment influenced only extractable P and NO_3^-, TN, and microbial C:N. Fertilization of soil increased extractable P significantly (soil P: $P < 0.01$) (Figure 3.2). Values for extractable P ranged from 21-41 $kg \cdot ha^{-1}$ for the soil P treatment and from 2-5 $kg \cdot ha^{-1}$ for the control. Overall, extractable P was ~445-2700% greater in the soil P treatment than in the control. Soil P fertilization ($P = 0.04$) resulted in lower NO_3^- (Figure 3.1). Values for NO_3^- ranged from 1.09-1.48 $k \cdot gha^{-1}$ (soil P) and from 1.23-3.02 $k \cdot gha^{-1}$ (control). Values for NO_3^- were ~47-88% lower in the soil P treatment than the control. Both the plant P and soil P treatments were significant for TN and microbial C:N, but only within the context of site (site × plant P × soil P: $P = 0.04$ for both pools). All other soil pool variables differed only with respect to site and/or time, with no P treatment effects. See Tables 3.2 and 3.3 for mineral soil properties for the control and soil P treatment, respectively.

Mass loss dynamics and decomposition rates

There were no effects of the P treatments with respect to PMR (Figure 3.3). The litter type × time interaction was significant ($P < 0.01$) for PMR and these individual effects were both highly significant on their own ($P < 0.01$), indicating differences in decomposition patterns among foliage, twigs, and roots.

The soil P treatment had a slight effect on k_e values with respect to litter type, resulting in foliage in the soil P treatment decomposing at a slower rate than foliage in the other treatments (soil P × litter type: P = 0.03). Foliage k_e values were ~23-50% higher than roots and 31-60% higher than twigs, corresponding to decomposition that was 1.3-2 times faster than roots and 1.8-2.4 times faster than twigs (Table 3.4). Values for k_e for foliage in the soil P treatment ranged from 0.566-0.710 yr^{-1}, whereas k_e values for foliage in the other treatments ranged from 0.619-0.870 yr^{-1}. Root k_e values were similar across treatments, ranging from 0.379-0.575 yr^{-1}. Twig k_e values were also similar across treatments and ranged from 0.313-0.456 yr^{-1}. Site and litter type ($P < 0.01$ for both effects) were also significant effects for k_e comparisons. With respect to site, site 39 exhibited higher k_e values (faster decomposition) than the other 2 sites.

Litter nutrient dynamics

Fertilization of seedlings with P influenced initial N and P content, but not initial C content (litter type × treatment: $P < 0.01$ for all variables except C content). Initial litter N concentrations were ~9%, 20%, and 63% higher in P-fertilized litter for foliage, roots, and twigs respectively and ranged from 8-17 $mg \cdot g^{-1}$, with twigs representing the low end of the range and foliage the high end (Table 3.5). Initial P concentrations were ~452%, 118%, and 184% greater for foliage, roots, and twigs from P-fertilized seedlings and ranged from 1.5-1.6 $mg \cdot g^{-1}$ (control) and 4-9 $mg \cdot g^{-1}$ (fertilized). All three initial mass-based element ratios were lower for fertilized litter for all litter types. Values for initial C:N ranged from 30-51 and were ~9-40% lower for P-fertilized litter. Foliage had the lowest C:N and twigs the highest. P-fertilized

litter C:P values were 56-84% lower than control litter and ranged from 60-380. Control litter C:P values were similar across litter types, but C:P of fertilized foliage was approximately half of the values for roots and twigs. For initial N:P, fertilized litter ratios were 42-82% lower than control litter. Values for N:P ranged from 2-11, with foliage exhibiting the highest ratios and twigs the lowest. For initial C concentrations, only the individual effect of litter type ($P < 0.01$) was significant, with foliage containing slightly more C than roots or twigs. Initial C concentration values ranged from 489-512 $mg \cdot g^{-1}$ (Table 3.5).

All results presented below for nutrient concentrations, nutrient release, and element ratios are for final values of these variables after 2 years of decomposition. Litter P content, but not soil P, influenced N and P concentrations of decomposing litter but did not influence C concentrations. The N concentration of decomposing litter samples after 2 years was still highest for P-fertilized litter, being significantly influenced by litter P content and litter type ($P < 0.01$ for both plant P and litter type effects). Specifically, the N concentration of litter in the plant P treatment was ~2-10% greater than control litter for foliage, and ~2-14% and ~10-40% greater for roots and twigs respectively. N concentrations ranged from 20-29 $mg \cdot g^{-1}$ (foliage), 16-20 $mg \cdot g^{-1}$ (roots), and 9-13 $mg \cdot g^{-1}$ (twigs) (Table A2.1). For foliage and roots, these concentrations were ~23-42% (foliage) and ~40% (roots) greater than the initial N concentrations. Litter P concentrations were significantly affected only by litter type ($P < 0.01$), with foliage exhibiting the highest concentrations and twigs the lowest (Table A2.1). P concentrations ranged from 1.2-2 $mg \cdot g^{-1}$ (foliage), 1.1-1.6 $mg \cdot g^{-1}$ (roots), and 0.4-0.9 $mg \cdot g^{-1}$ (twigs). With respect to initial P concentrations, P-

fertilized litter concentrations were ~81% (foliage), ~83% (roots), and ~92% (twigs) less than initial P concentrations in fertilized litter.

Fertilization with P (both plant and soil) influenced element release from decomposing litter for C, N, and P. Release of C was dependent upon both litter P and soil P within the context of site and litter (site × plant P × soil P × litter type: $P < 0.01$). Generally, litter in the control released ~10-32% (foliage) and ~9-13% (roots) more C than litter in the plant P × soil P treatment (Figure 3.4). Overall, foliage released ~45-69%, roots released ~37-50%, and twigs released ~18-68% of initial C (Table A2.2). Both the plant and soil P treatments influenced net N mineralization, but with only with respect to litter type ($P < 0.01$ for both plant P × litter type and soil P × litter type). For foliage, control litter generally released ~30-64% more N than litter in the three P treatment groups. Net N mineralization from roots did not exhibit a pattern with respect to treatment and varied across sites. In contrast to foliage, twig litter in the P treatments mineralized ~30-106% more N than in the control (Figure 3.5). Litter type ($P < 0.01$) was highly significant on its own for net N mineralization, with foliage releasing the most N and roots the least N independent of any P treatment. Overall, foliage mineralized ~19-55% of initial N, roots mineralized ~0.5-19%, and twigs mineralized ~21-79% after 2 years of decomposition (Table A2.2). Litter P content influenced net P mineralization and was greatest for litter in the plant P and plant P × soil P treatments for all litter types (plant P × soil P × litter type: $P = 0.04$). Net P mineralization from foliage was ~19-35% greater in these two treatments than in the control and ~37-62% greater than in the soil P treatment. For roots, litter in the plant P and plant P × soil P treatments mineralized ~16-32% more P than in the

control or soil P treatment. Net P mineralization from twigs was ~10-31% and greater for the plant P and plant P × soil P treatments than the control or soil P treatment (Figure 3.6). In addition, the individual effect of plant P was highly significant ($P < 0.01$) on its own with respect to net P mineralization. As for net N mineralization, litter type ($P < 0.01$) was also highly significant on its own with respect to P mineralization. Foliage mineralized 3~5-93%, roots mineralized ~55-81%, and twigs mineralized ~64-96% of initial P over 2 years of decomposition (Table A2.2).

Predicted N mineralization patterns generated using the LIDET model were very similar to the observed patterns of N mineralization for my study, particularly for foliage and roots (Figure 3.7). This is in contrast to my findings in Chapter 2, in which the LIDET model underestimated N release. In Chapter 2, I discussed that the LIDET model was perhaps not optimized for root and twig litter since its parameters were derived from leaf litter data. However, in my P-fertilization study, the LIDET model fits well with the observed root data. This suggests that for this study, initial litter chemistry was exerting strong control over the N dynamics of the decomposing litter, perhaps even more so than in the ^{15}N study (Chapter 2).

Litter element ratios shifted over the course of the study, with C:N decreasing, C:P either increasing or decreasing, and N:P increasing. Litter P content (plant P: $P = 0.01$) significantly influenced C:N and as did litter type ($P < 0.01$) , whereas litter C:P differed only with respect to litter type ($P < 0.01$). With respect to treatments without P-fertilized litter (control and soil P), C:N values were ~27-56% (foliage), ~60-91% (roots), and ~4-52% (twigs) lower than initial C:N values. Treatments receiving P-fertilized litter had C:N values ~35-50%, ~50-64%, and ~9-38% lower than initial C:N

values with respect to foliage, roots, and twigs. Overall, C:N values ranged from 20-26, 25-32, and 36-64 for foliage, roots, and twigs respectively. Even though there were no significant effects of plant or soil P fertilization with respect to C:P, C:P values for P-fertilized litter after 2 years were ~81%, ~58%, and ~84% higher than initial C:P values for P-fertilized litter for foliage, roots, and twigs respectively. For control litter, C:P values were ~6-25% (roots) and ~64% (twigs) higher than initial values but 1-34% lower than initial C:P for foliage. Values for C:P at the end of the study ranged from 250-446 (foliage), 323-455 (roots), and 640-1494 (twigs). After 2 years, N:P values were higher than initial values for all treatments, with treatments containing P-fertilized litter exhibiting the greatest changes in N:P (plant P × soil P × litter type: $P = 0.05$). For N:P, values were ~14-39% (foliage), ~51% (roots), and ~67% (twigs) higher than initial N:P in the control and soil P groups, which did not contain P-fertilized litter. The plant P and plant P × soil P treatments resulted in litter N:P values ~87%, ~73%, and ~81% higher than initial values. Litter type ($P < 0.01$) was also significant for N:P, with ratios ranging from 13-19 (foliage), 12-16 (roots), and 15-23 (twigs) at the end of the study (Table A2.3).

Values for k_e, N release, and P release, were all strongly correlated ($P \leq 0.01$) with initial litter element concentrations and ratios. N release correlated best with initial litter N concentrations, and P release correlated best with initial litter P. Additionally, N release and P release were strongly correlated ($P < 0.01$) (Table A2.4).

DISCUSSION

The objective of this study was to examine the relationships among P availability, mass loss dynamics, and N and P release patterns of decomposing litter.

To achieve this objective, fertilizer was applied separately to seedlings harvested for litter materials and to soil in the field, to increase the P content of both litter and soil pools. In fertilization studies, the absence of an effect can on occasion be attributed to the application of fertilizer in an amount too low to overcome any nutrient limitations in the system being studied. However, in this study both fertilization of the seedlings and soil produced marked differences between the treatment and control groups, indicating that the fertilization treatment was effective. Additionally, the litter used for this study was fresh litter from seedlings. Although P-fertilization of seedlings influenced initial N and P concentrations in litter used for this study, both P-fertilized litter and control litter had higher N and P concentrations for a given litter type than other values reported in the literature for litterfall (Sollins et al. 1980) or litter typically used in decomposition studies, many of which used senesced litter (e.g. Hobbie and Vitousek 2000, Prescott et al. 2004). Thus, the results from my study may be influenced by the higher N and P concentrations of the litter used and further by the use of litterbags which may result in slower mass loss due to the separation of the decomposing material from the surrounding litter layer or soil (Dornbush et al. 2002).

Decomposition and P availability

For a given litter type, decomposition varied little across sites and treatments, suggesting that P availability exerted only minor control over mass loss dynamics. Decomposition rate constants were slightly lower for foliage decomposing in plots fertilized with P (soil P treatment), but this did not translate to noticeable differences in percent mass remaining (PMR) at 2 years with respect to P fertilization of either litter or soil. Decomposition rates were slightly higher at site 39. Of the three sites,

this site had the greatest soil N availability which could contribute to faster decomposition at this site. A study of decomposition along the Hawaiian chronosequence (Crews et al. 1995) showed that decomposition of foliage is faster at sites with greater N and P availability, but only when both soil and litter nutrients where considered (Hobbie and Vitousek 2000). Given the high N and P concentrations of the control litter used in this study, my results suggest that at site 39 greater soil P availability (from fertilization) coupled with greater soil N availability worked synergistically with litter nutrients to increase decomposition rates. Given the similarities in soil P availability across sites but lower soil N availability for sites 5 and 58, the lower k_e values for these two sites are in agreement with a coupled effect of soil P and N availability on decomposition rates as well as a coupling of the effects of soil and litter nutrient availability. This suggested interaction between soil N and P availability and decomposition rate both supports and contrasts findings from other decomposition studies that have examined nutrient limitations to decomposition. Matkins (personal communication) found both soil N fertilization and high foliar litter N concentrations negatively influenced decomposition rates of Douglas-fir foliage in the Oregon Coast Range. Further, litter calcium (Ca) and N were negatively related and thus there was strong positive relationship between litter Ca concentrations and decomposition rates (Matkins, personal communication). Another study along the Hawaiian chronosequence examining foliage and root decomposition found that foliage decomposed faster at the most nutrient-rich site and that roots decomposed faster at the most nutrient-rich site as well as the low N availability site (Ostertag and Hobbie 1999). Further, fertilization with N and P increased decomposition rates for

roots, but only at the oldest, most nutrient-limited site, suggesting that root decomposition at the oldest site was limited by N and P (Ostertag and Hobbie 1999). Similar results for the interaction between fertilization and decomposition were reported from a separate study on fine root dynamics at the same sites in Hawaii (Ostertag 2001). In contrast, P fertilization did not significantly influence mass loss of foliage at P-limited sites in Costa Rica (Cleveland et al. 2006) or Brazil (McGroddy et al. 2004b).

Given that these studies were undertaken in different ecosystems (e.g. dry tropical versus wet tropical versus temperate), it is understandable that a clear pattern describing decomposition relative to soil P availability (or nutrient availability in general) has not emerged. Further, while soil P and/or N availability may influence decomposition rates, this influence may be directly constrained by site- or ecosystem-specific attributes such as litterfall inputs and temperature and precipitation regimes. With respect to sites in the Oregon Coast Range, it seems that low soil N availability or low litter N concentrations are not limiting to decomposition and that high soil or litter N may inhibit decomposition, whereas P availability (litter or soil) has little influence on decomposition rates. Thus, this raises the question of what could potentially limit decomposition in the Oregon Coast Range if it is not N or P. The interesting relationships between litter calcium and N concentrations and decomposition rates found by Matkins (personal communication) suggest a potential limiting role of Ca. Of the three sites used for my study, site 39, in addition to having the highest N availability, also has the lowest exchangeable Ca (Perakis et al. 2006). The triple superphosphate fertilizer used to fertilize the soil added ~140 $kg \cdot ha^{-1}$ Ca to

the fertilized plots. Thus, the slight increase in decomposition rates at this site may be potentially be attributed to increased soil Ca from fertilization rather than high inherent soil N availability at the site.

Litter nutrient dynamics

P fertilization had a stronger effect on litter nutrient dynamics than it did on decomposition rates. Litter nutrient concentrations, nutrient mineralization patterns, and element ratios all responded to some degree to treatments with P-fertilized litter and/or P fertilization of soil. After 2 years of decomposition P-fertilized litter had greater N concentrations but lower P concentrations than unfertilized control litter. All litter types exhibited rapid mineralization of P within the first 3 months of decomposition for all treatments, though P-fertilized litter mineralized a greater percentage of initial P than litter in the control or soil P treatment. However, after 2 years litter P concentrations were similar across treatments despite the differences in P mineralization. Fertilization of both litter and soil had mixed effects on the release of C and N due to the influence of litter type. These results are consistent with Hobbie and Vitousek (2000), in which both fertilization of litter (foliage only) and soil with N and P influenced litter dynamics. With respect to fertilized litter, they found that N dynamics were less influenced by fertilization treatments than P dynamics. At young (N- and P-limited) and old (P-limited) sites in Hawaii, N was immobilized independent of fertilization treatment, while at the intermediate site (nutrient rich), N was mineralized from decomposing foliage (Hobbie and Vitousek 2000). However, litter with elevated N concentrations tended to immobilize P while litter with elevated P concentrations tended to release P at both the young and old sites (Hobbie and

Vitousek 2000). Soil fertilization with N and P also influenced nutrient dynamics of fine roots decomposed at the same sites in Hawaii. Fine roots immobilized N in both soil N- and P-fertilized treatments at the young and old sites. However, roots mineralized P in the soil P-fertilized treatments at both sites, but immobilized P in the N-fertilized treatment at the old site (Ostertag and Hobbie 1999). Fertilization of soil with P also increased P immobilization in decomposing foliage in P-rich and P-limited sites in Costa Rica and P-limited sites in Brazil (Cleveland et al. 2006, McGroddy et al. 2004). In my study, N immobilization occurred in the early stages of decomposition for twigs and roots, after which the general pattern for all litter types and treatments was one of N release. For P, the general pattern was net mineralization with little immobilization. Foliage at two of the sites in the soil P treatment exhibited P immobilization, but given the P mineralization results for all other treatments and litter types it seems likely that soil adhering to the litter samples inflated the P content of these particular samples.

If soil nutrient availability does influence litter nutrient dynamics, then the rapid mineralization of P from decomposing litter, even in the control treatment, compared to the slower mineralization of N suggests that decomposition at these sites is relatively more N-limited than P-limited. Another explanation for the rapid loss of P could be the high initial litter P concentrations. In the Canadian Intersite Decomposition Experiment (CIDET), litter with higher initial P concentrations mineralized more P than litter with lower initial P concentrations (Moore et al. 2006). Given that even control litter in my study had relatively high P concentrations, this could have potentially resulted in the rapid mineralization of P from litter independent

of soil P availability. Since P in plants is generally contained in metabolic forms, as opposed to being structurally-bound (Taiz and Zeiger 2002), this may have facilitated the rapid mineralization of P from the litter through the leaching of readily-accessed P-containing metabolic compounds. The slower rate of N mineralization and evidence of N immobilization is in contrast to a comparative study of N dynamics in multiple litter types using ^{15}N (Chapter 2) in which all litter types showed mineralization of N. Release of N from litter has been shown to be related to initial litter N concentration (Berg and Ekbohm 1983, Stohlgren 1988, Chen et al. 2002, Parton et al. 2007). However, the initial N concentrations for the litter used in this study were comparable to the litter used in the ^{15}N study (Chapter 2). This suggests that other factors were controlling N mineralization in addition to or instead of initial litter N concentration. Predicted N mineralization patterns generated using the LIDET model were very similar to the observed patterns of N mineralization for my study, particularly for foliage and roots (Figure 3.7). This is in contrast to my findings in Chapter 2, in which the LIDET model underestimated N mineralization. In Chapter 2, I discussed that the LIDET model was perhaps not optimized for root and twig litter since its parameters were derived from leaf litter data. However, in my P-fertilization study, the LIDET model fits well with the observed root data. This suggests that for this study, initial N concentration was exerting strong control over the N dynamics of the decomposing litter, perhaps even more so than in the ^{15}N study (Chapter 2). However, this explanation is inconsistent with the correlations between N mineralization and initial N concentrations, as this correlation was much stronger for the ^{15}N data (Chapter 2) than for the data presented in here in Chapter 3. If soil nutrient

availability was influencing litter nutrient dynamics as suggested above, then this pattern of N mineralization and immobilization suggests that these sites are relatively more N-limited than P-limited with respect to litter nutrient dynamics during decomposition. In addition, soil NO_3^- was lower in the soil P treatment, suggesting immobilization of NO_3^- and potential N-limitation since it is unlikely leaching of NO_3^- would occur preferentially from these three plots at each site and lower NO_3^- levels. Although lower NO_3^- in only the soil P treatment cannot account for the N mineralization patterns across the other treatments, this indicates that soil P fertilization may have potentially induced N-limitation of decomposers (e.g., microbes) at the plot level which resulted in lower rates of N mineralization. This supports the idea that soil nutrient availability may influence nutrient mineralization from decomposing litter.

Coupling of element cycles

The most striking results of this study are the shifts in element ratios over the course of 2 years of decomposition. Due to P fertilization of seedlings and the consequent increases in N and P concentrations in initial litter, initial litter element ratios in P-fertilized litter were lower than the control litter ratios. However, over the course of 2 years, element ratios within a given litter type generally converged across treatments, particularly with respect to C:N and N:P. Values for C:N decreased, which is consistent with lower rates of N release compared to C release and also N immobilization in the decomposing litter. Values for N:P increased, most likely due to the rapid release of P compared to N. Shifts in C:P were less consistent across litter

types. These results suggest a closer coupling of both C and N cycling and N and P cycling compared to C and P cycling.

The convergence of the different element ratios to similar values across treatments within a given litter type suggests these elements are similarly constrained and that nutrient transformations during decomposition are regulated to maintain these specific ratios. Global estimates of foliar ratios for temperate coniferous forests range from 45-58, 423-531, and 9-11 for C:N, C:P, and N:P respectively. Mass-based foliar litter ratios for temperate coniferous forests range from 69-81, 775-1046, and 10-14 for C:N, C:P, and N:P (global mass-based ratios converted from molar ratios from McGroddy et al. 2004a). For this study, C:N values after 2 years are lower than the global estimates for both foliage and foliar litter , most likely due to the high initial N concentrations in the fresh litter used compared to older foliage or senesced foliage that may have had N translocated from the tissue. Similarly, C:P values for this study are lower than the global estimates for both foliage and litter. Again, even though a large proportion of P was released from the litter, initial P concentrations may have been high enough to maintain lower C:P ratios. In contrast, N:P values for this study are slightly higher than the global estimates for foliage and litter, but similar to N:P values for foliage decomposed in the CIDET study (Moore et al. 2006) as well decomposing logs (Sollins et al. 1987). Thus, the results for litter element ratios in this study are in agreement with the idea that biomass and litterfall in forest ecosystems tend to converge towards predictable element ratios (McGroddy et al. 2004a, Moore et al. 2006).

Conclusions and implications

This is the first study to address relationships between soil P availability, litter P concentrations, decomposition, and litter nutrient dynamics in temperate coniferous forests. The results demonstrate that these relationships are complex and vary with respect to different litter types. Litter nutrient concentrations seem to exert greater control over decomposition rates and litter nutrient dynamics, although soil nutrient availability may also influence litter nutrient dynamics. Although we tend to think of individual element cycles (e.g. C, N, and P), this study suggests that these element cycles are similarly constrained and that N and P cycling may be closely coupled. It is possible that physiological mechanisms in soil biota may work to maintain specific element ratios in litter that most likely optimize nutrient availability. The process of maintaining these ratios could result in transformations of these elements (particularly N and P) that may be predictable given litter N and P concentrations and soil N and P availability. These transformations will have implications for fluxes of N and P within a forest ecosystem as well as fluxes between ecosystems as these elements cycle through the plant-soil continuum.

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FIGURES

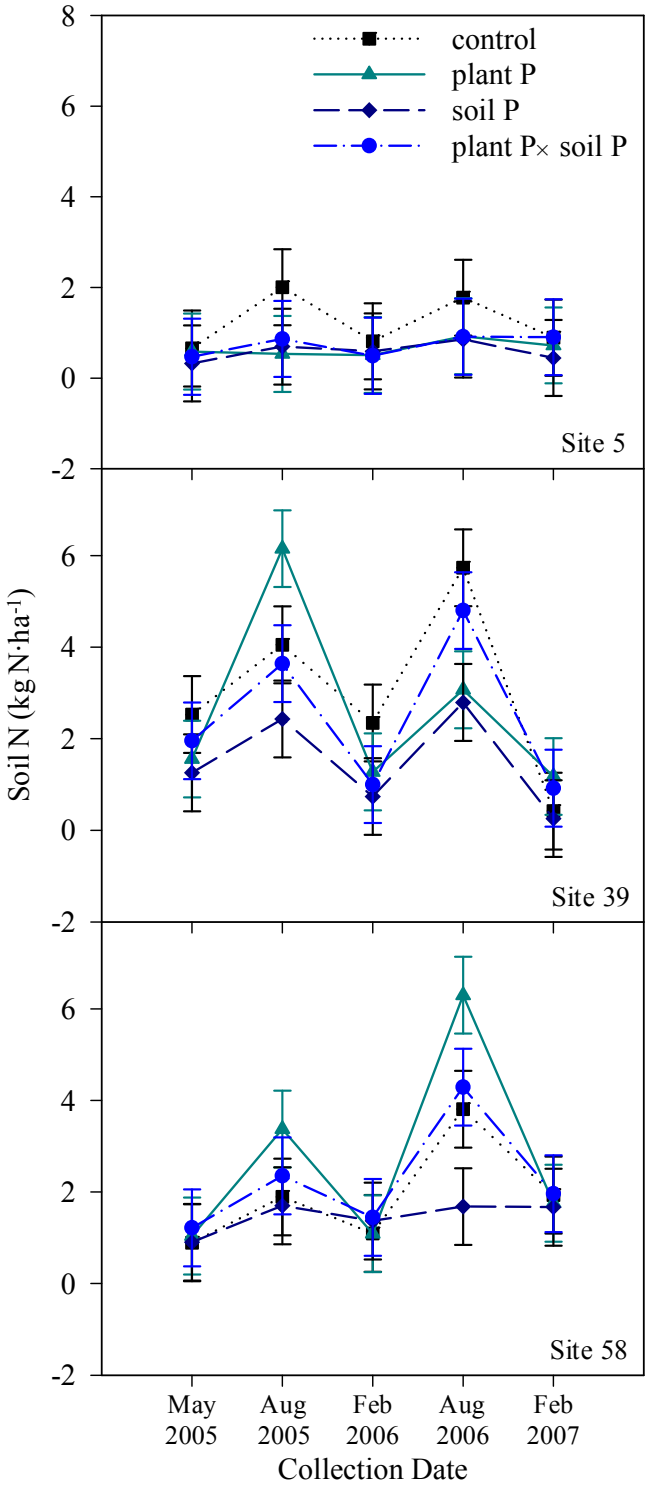

Figure 3.1. Extractable soil N (as NO_3^-) for the three sites in the Oregon Coast Range where litter was decomposed. Treatments are plant P (P-fertilized litter), soil P (P-fertilized soil), and plant P × soil P. Values are means ± SE, $n = 3$.

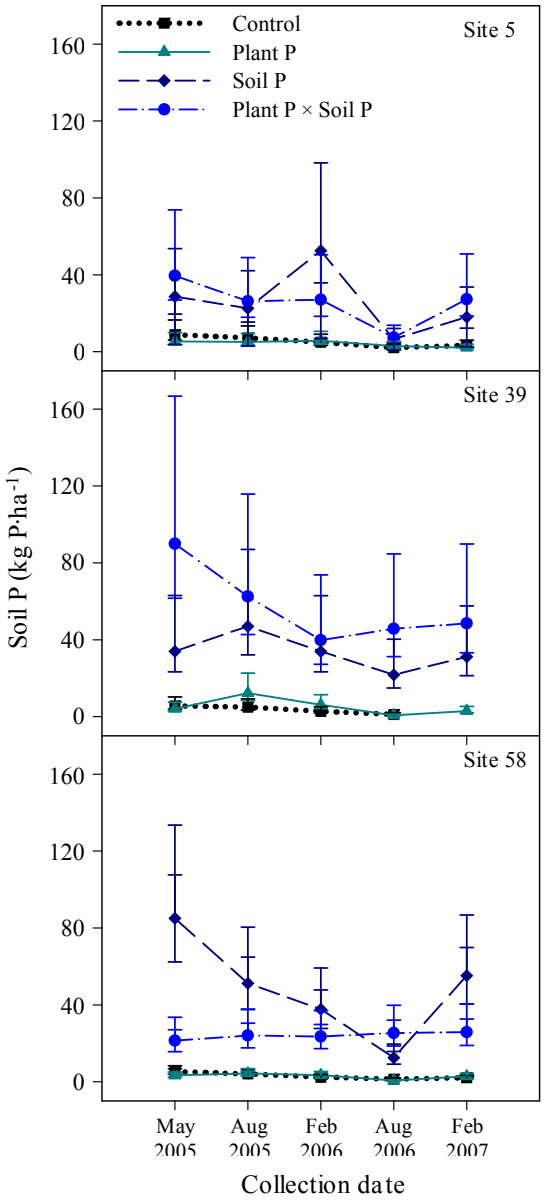

Figure 3.2. Extractable soil P for the three sites in the Oregon Coast Range where litter was decomposed. Treatments are plant P (P-fertilized litter), soil P (P-fertilized soil), and plant P × soil P. Values are means ± SE, $n = 3$.

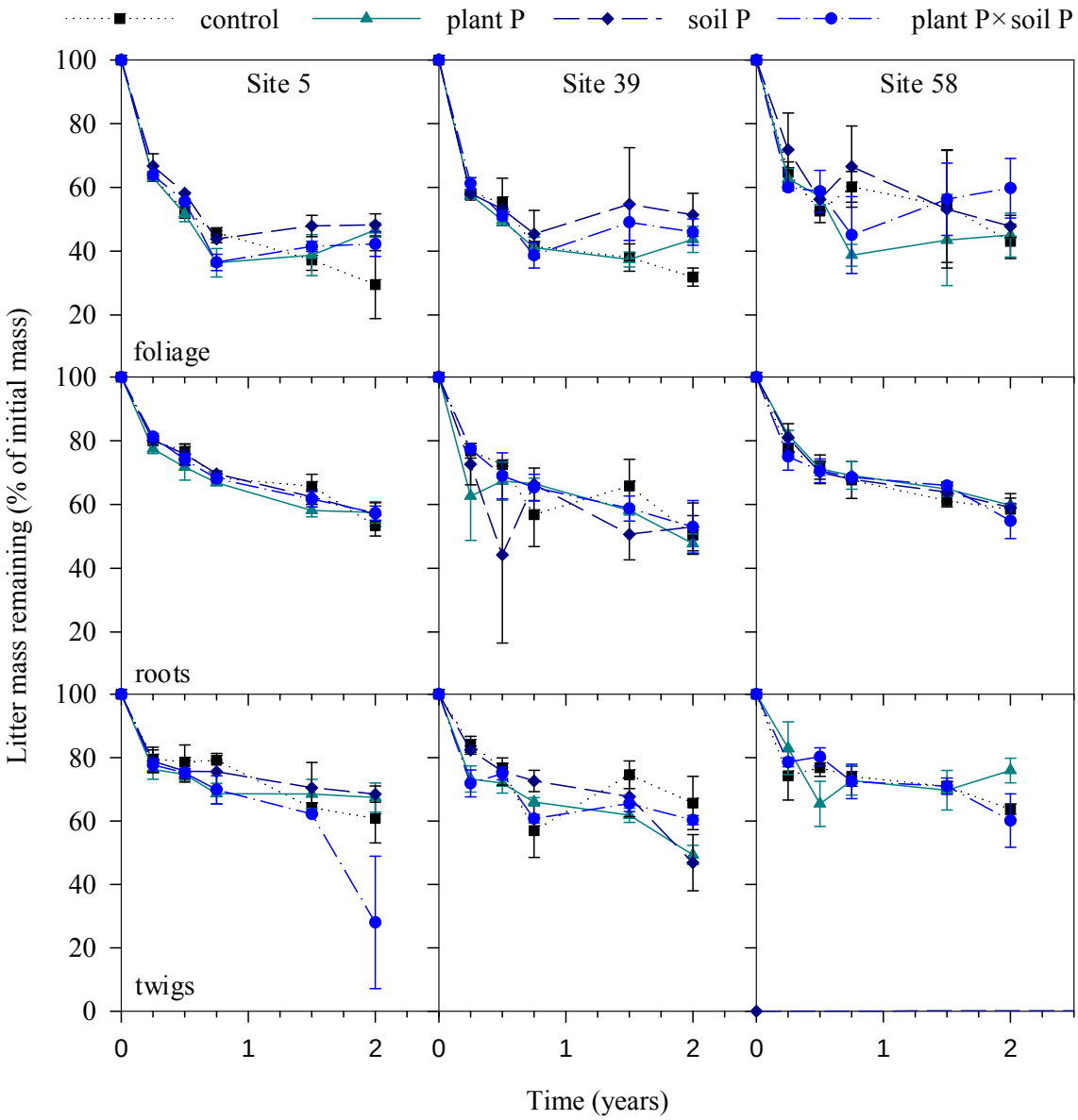

Figure 3.3 Litter mass remaining (as percent of initial mass) for litter decomposed at three sites in the Oregon Coast Range. Treatments are control (no P fertilization), plant P (P-fertilized litter), soil P (P-fertilized soil), and plant P × soil P. Columns correspond to site and rows correspond to litter type. Values are means ± SE, $n = 3$.

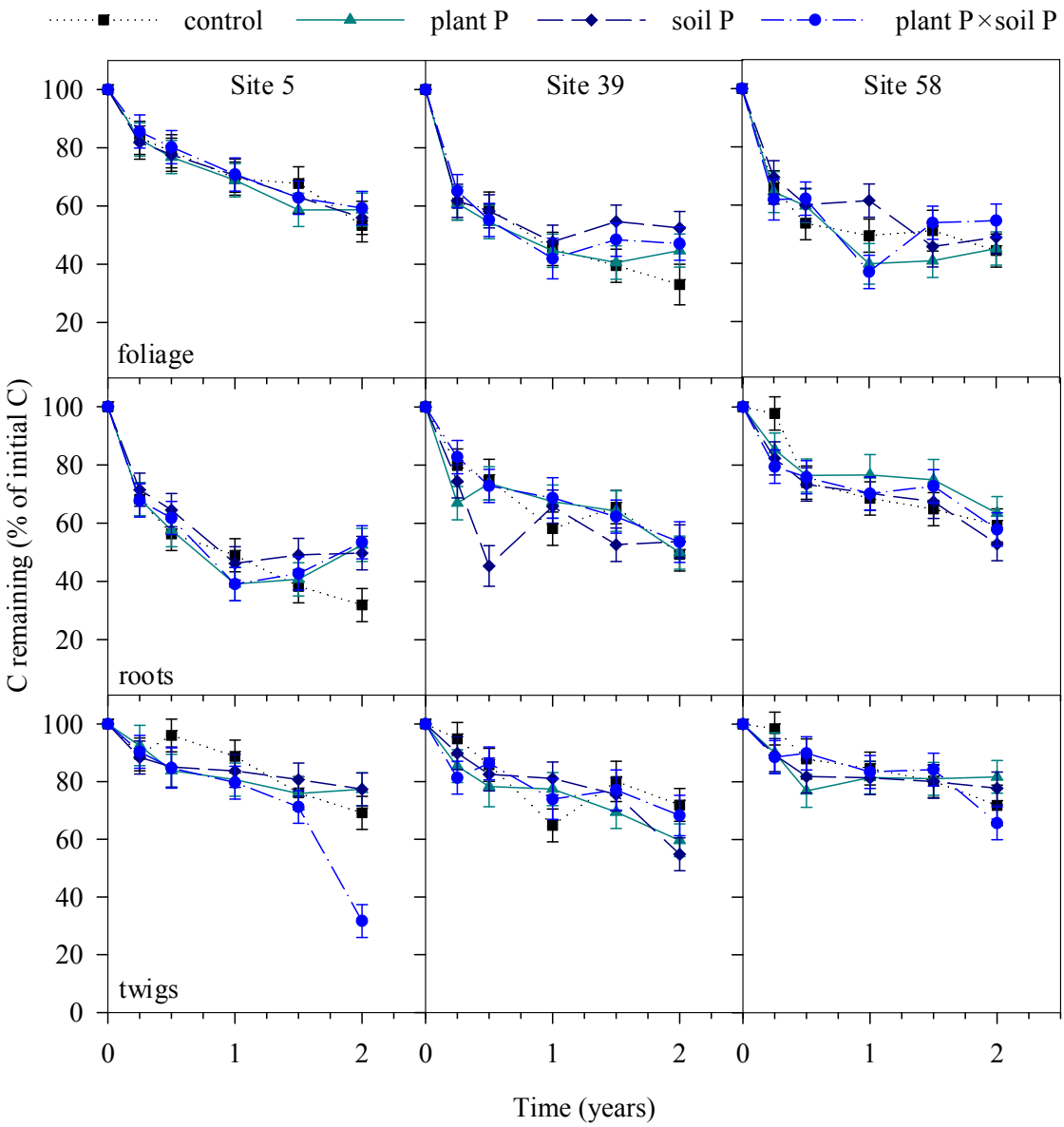

Figure 3.4. C remaining (as percent of initial C) for litter decomposed at three sites in the Oregon Coast Range. Treatments are control (no P fertilization), plant P (P-fertilized litter), soil P (P-fertilized soil), and plant P × soil P. Columns correspond to site and rows correspond to litter type. Values are means ± SE, $n = 3$.

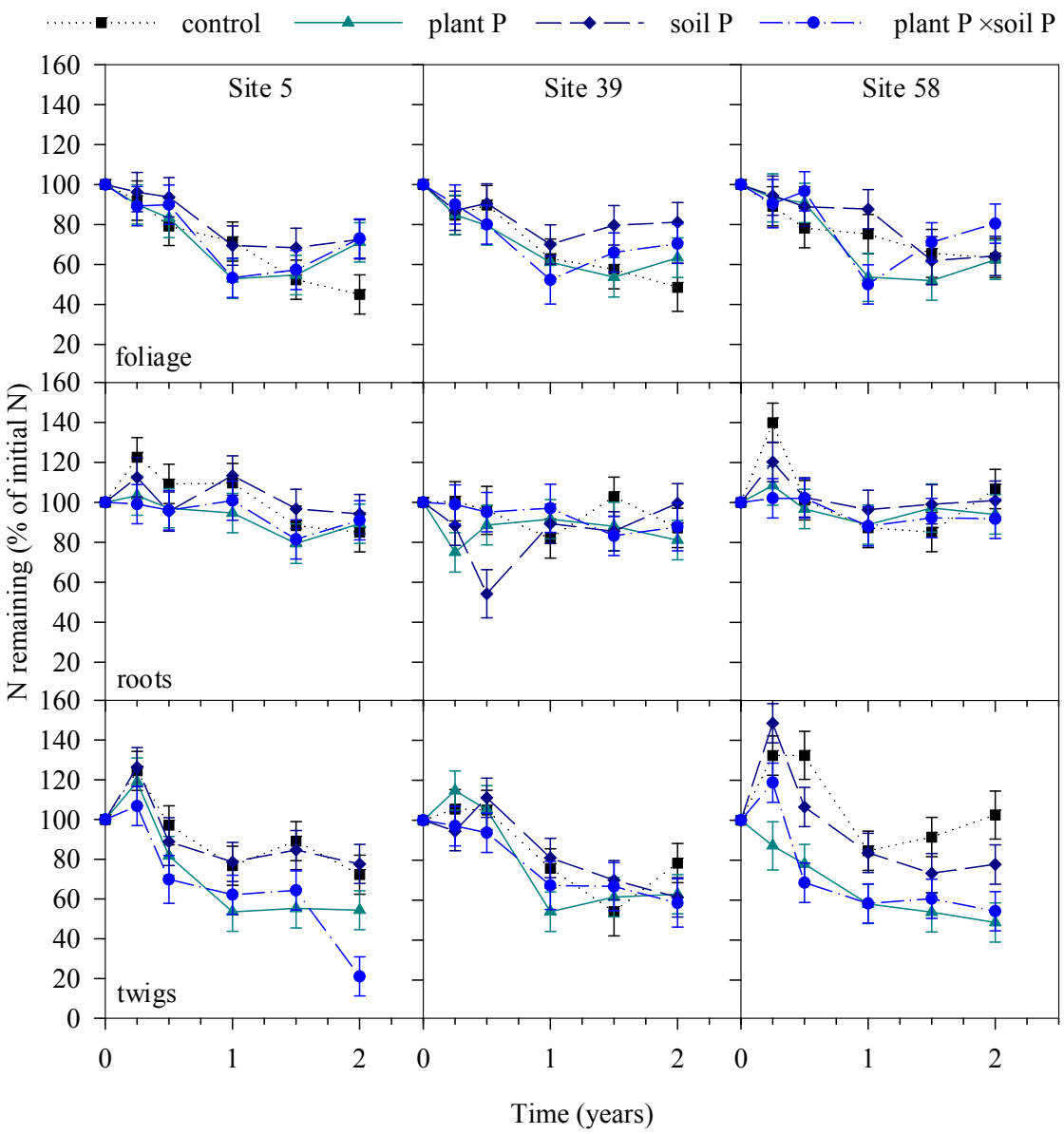

Figure 3.5. N remaining (as percent of initial N) for litter decomposed at three sites in the Oregon Coast Range. Treatments are control (no P fertilization), plant P (P-fertilized litter), soil P (P-fertilized soil), and plant P × soil P. Columns correspond to site and rows correspond to litter type. Values are means ± SE, $n = 3$.

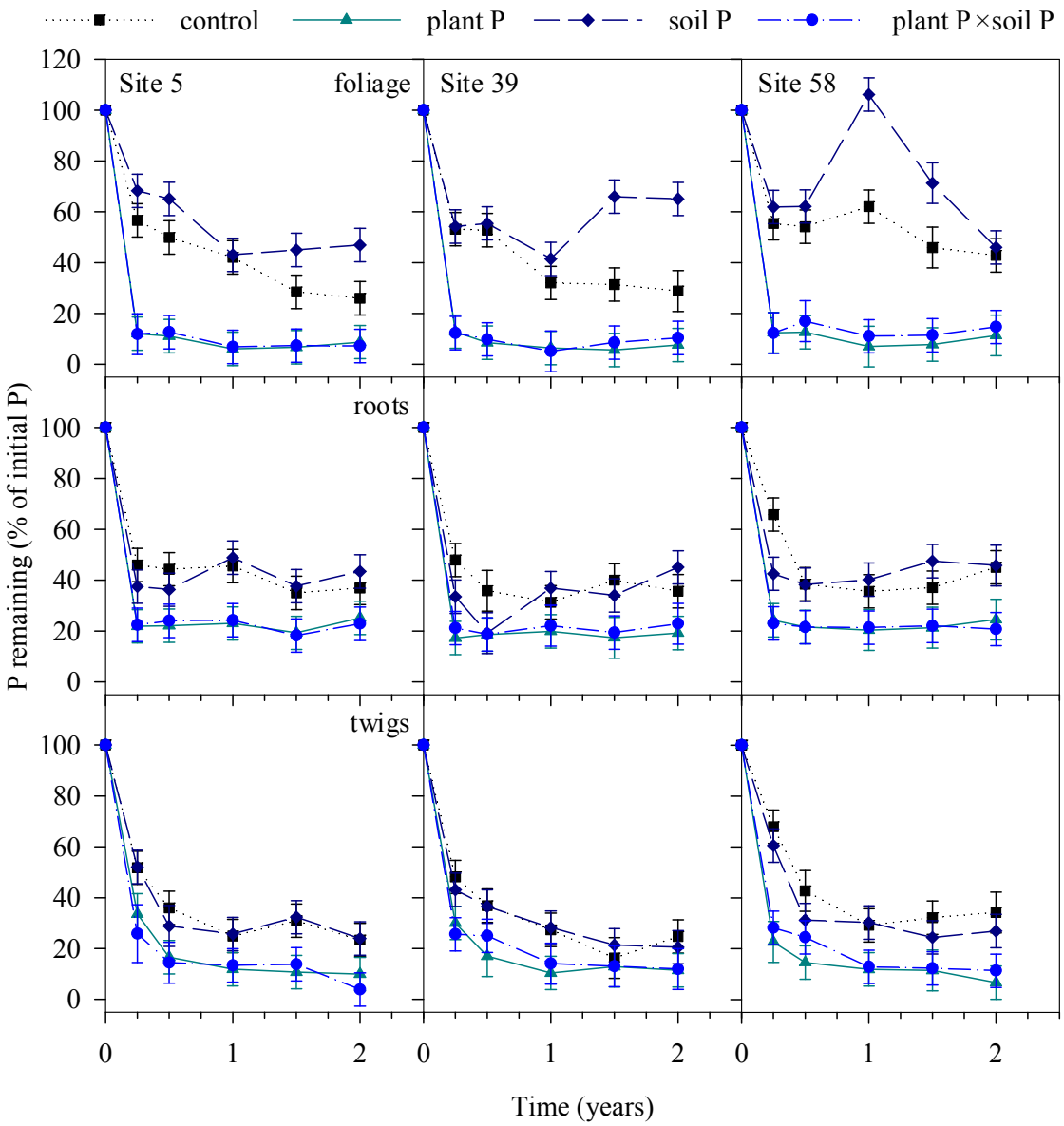

Figure 3.6. P remaining (as percent of initial P) for litter decomposed at three sites in the Oregon Coast Range. Treatments are control (no P fertilization), plant P (P-fertilized litter), soil P (P-fertilized soil), and plant P × soil P. Columns correspond to site and rows correspond to litter type. Values are means ± SE, $n = 3$.

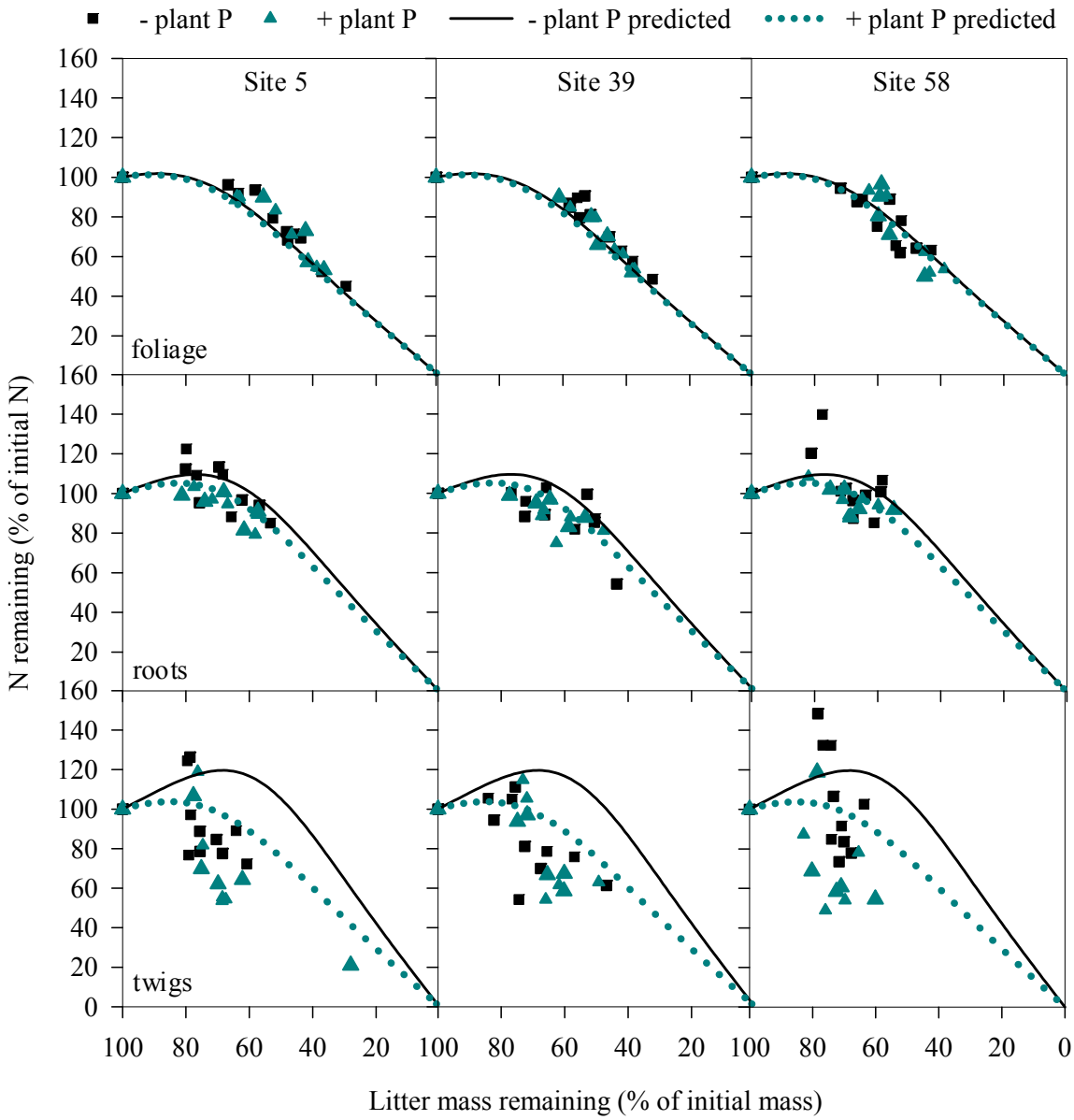

Figure 3.7. Observed net N mineralization (as percent of initial N) versus percent of initial mass remaining for litter decomposed at three sites in the Oregon Coast Range. For the purpose of this figure, the four treatment groups used in the study (control, plant P, soil P, plant P × soil P) were combined into two groups based on whether they received P-fertilized litter: - plant P (control and soil P data) and + plant P (plant P and plant P × soil P data). Lines are predicted N mineralization patterns as a function of initial litter N concentration and mass remaining based on an equation derived from data from the Long-Term Intersite Decomposition Experiment (LIDET) (Parton et al. 2007).

TABLES

Table 3.1. Site characteristics.

Site characteristic	Site 5	Site 39	Site 58
Location	44º38’ N, 123º48’ W	45º44’ N, 123º53’ W	44º43’ N, 123º49’ W
Distance from ocean (km)	16	4.5	20
Elevation (m)†	322	23	80
MAP (mm) †	1730	2000	1750
MAT (ºC)†	11.2	10.3	10.8
Slope (%)†	55	10	15
Aspect (º)†	220	160	75
Parent material	Sandstone	Sandstone	Sandstone
Soil subgroup (USDA)‡	Andic Dystrudepts	Andic Dystrudepts	Andic Dystrudepts

† Maguire et al. (2002) unpublished data.

‡ Current soil classification based on Benton County and Tillamook County NRCS Soil Surveys.

Table 3.2. Mineral soil properties for controls (no plant or soil P fertilization) at three sites in the Oregon Coast Range.

Property	Units	Site 5	Site 39	Site 58
Bulk density*	$g \cdot cm^{-3}$	0.42	0.47	0.58
pH	2:1 H_2O:soil	5.50 ± 0.08	4.44 ± 0.08	4.93 ± 0.08
Soil moisture	%	37.57 ± 0.98	43.47 ± 0.98	33.19 ± 0.98
DOC**	$kg \cdot ha^{-1}$	77.10 ± 13.88	134.63 ± 13.88	215.11 ± 13.88
Extractable NH_4^+-N	$kg \cdot ha^{-1}$	0.96 ± 0.73	1.36 ± 0.73	0.94 ± 0.73
Extractable NO_3^--N	$kg \cdot ha^{-1}$	1.23 ± 0.51	3.02 ± 0.51	1.93 ± 0.51
DIN†	$kg \cdot ha^{-1}$	2.18 ± 1.00	4.38 ± 1.00	2.87 ± 1.00
DON‡	$kg \cdot ha^{-1}$	4.11 ± 0.55	4.57 ± 0.55	9.34 ± 0.55
TDN^	$kg \cdot ha^{-1}$	4.53 (0.67, 0.95)	5.78 (0.85, 1.21)	10.19 (1.50, 2.13)
Microbial C	$kg \cdot ha^{-1}$	128.30 ± 17.70	165.76 ± 17.70	132.33 ± 17.70
Microbial N	$kg \cdot ha^{-1}$	24.76 ± 2.69	30.64 ± 2.69	32.94 ± 2.69
Microbial C:N	mass:mass	5.03 (0.28, 0.32)	5.23 (0.30, 0.33)	2.40 (0.15, 0.17)
Total C	$kg \cdot ha^{-1}$	54,403 (3,462, 3,967)	48,481 (2,962, 3,374)	55,361 (3,382, 3,853)
Total N	$kg \cdot ha^{-1}$	2,659 ± 175	3,319 ± 175	2,719 ± 175
C:N	mass:mass	20.45 (1.66, 1.98)	14.86 (1.17, 1.39)	20.72 (1.63, 1.93)
Extractable PO_4^{3-}-P	$kg \cdot ha^{-1}$	4.56 (0.94, 1.60)	1.51 (0.54, 0.93)	1.51 (0.54, 0.93)

Notes: Values are means ± SE; $n = 15$ (values represent means for 3 plots × 5 collections at each site). For TDN, microbial C:N, total C, total N, C:N, and extractable P values are back-transformed means (lower SD, upper SD).

*Sinkhorn (2007).

** Dissolved organic carbon.

† Dissolved inorganic nitrogen (extractable NH_4^+-N + extractable NO^{3-}-N).

‡ Dissolved organic nitrogen.

^ Total dissolved nitrogen (DIN + DON).

Table 3.3. Mineral soil properties for soil P treatment at three sites in the Oregon Coast Range.

Property	Units	Site 5	Site 39	Site 58
Bulk density*	$g \cdot cm^{-3}$	0.42	0.47	0.58
pH	2:1 H_2O:soil	5.64 ± 0.08	4.63 ± 0.08	4.87 ± 0.08
Soil moisture	%	36.44 ± 0.98	41.08 ± 0.98	34.34 ± 0.98
DOC**	$kg \cdot ha^{-1}$	71.47 ± 13.88	138.52 ± 13.88	186.76 ± 13.88
Extractable NH_4^+-N	$kg \cdot ha^{-1}$	1.09 ± 0.73	1.41 ± 0.73	1.48 ± 0.73
Extractable NO_3^--N	$kg \cdot ha^{-1}$	0.58 ± 0.51	1.50 ± 0.51	1.46 ± 0.51
DIN†	$kg \cdot ha^{-1}$	1.67 ± 1.00	2.91 ± 1.00	2.95 ± 1.00
DON‡	$kg \cdot ha^{-1}$	4.50 ± 0.55	5.01 ± 0.55	9.25 ± 0.55
TDN^	$kg \cdot ha^{-1}$	4.18 (0.62, 0.87)	5.60 (0.83, 1.17)	11.10 (1.64, 2.32)
Microbial C	$kg \cdot ha^{-1}$	129.07 ± 17.70	127.32 ± 17.70	153.72 ± 17.70
Microbial N	$kg \cdot ha^{-1}$	26.35 ± 2.69	24.89 ± 2.69	35.16 ± 2.69
Microbial C:N	mass:mass	4.80 (0.27, 0.30)	4.79 (0.28, 0.31)	3.38 (0.19, 0.22)
Total C	$kg \cdot ha^{-1}$	49,496 (3,024, 3,445)	53,592 (3,274, 3,730)	51,675 (3,157, 3,597)
Total N	$kg \cdot ha^{-1}$	2,689 ± 175	2,802 ± 175	3,047 ± 175
C:N	mass:mass	18.52 (1.46, 1.73)	19.28 (1.52, 1.80)	17.21 (1.35, 1.60)
Extractable PO_4^{3-}-P	$kg \cdot ha^{-1}$	20.81 (4.29, 7.29)	30.54 (6.70, 11.40)	40.74 (8.39, 14.27)

Notes: Values are means ± SE; $n = 15$ (values represent means for 3 plots × 5 collections at each site). For TDN, microbial C:N, total C, total N, C:N, and extractable P values are back-transformed means (lower SD, upper SD).
*Sinkhorn (2007).
** Dissolved organic carbon.
† Dissolved inorganic nitrogen (extractable NH_4^+-N + extractable NO^{3-}-N).
‡ Dissolved organic nitrogen.
^ Total dissolved nitrogen (DIN + DON).

Table 3.4. Decomposition rate constants (k_e values) for foliage, roots, and twigs decomposed at three sites in the Oregon Coast Range.

Site	Litter type	Treatment†	k_e (yr^{-1})
5	Foliage	control	0.870 ± 0.09**
		plant P	0.866 ± 0.09**
		soil P	0.703 ± 0.09**
		plant P × soil P	0.838 ± 0.09**
	Roots	control	0.379 ± 0.04**
		plant P	0.432 ± 0.04**
		soil P	0.385 ± 0.04**
		plant P × soil P	0.395 ± 0.04**
	Twigs	control	0.327 ± 0.04**
		plant P	0.348 ± 0.04**
		soil P	0.308 ± 0.04**
		plant P × soil P	0.456 ± 0.04**
39	Foliage	control	0.998 ± 0.09**
		plant P	0.882 ± 0.09**
		soil P	0.710 ± 0.09**
		plant P × soil P	0.754 ± 0.09**
	Roots	control	0.459 ± 0.04**
		plant P	0.502 ± 0.04**
		soil P	0.543 ± 0.04**
		plant P × soil P	0.575 ± 0.04**
	Twigs	control	0.389 ± 0.04**
		plant P	0.444 ± 0.04**
		soil P	0.366 ± 0.04**
		plant P × soil P	0.408 ± 0.04**
58	Foliage	control	0.621 ± 0.09**
		plant P	0.764 ± 0.09**
		soil P	0.566 ± 0.09**
		plant P × soil P	0.619 ± 0.09**
	Roots	control	0.411 ± 0.04**
		plant P	0.383 ± 0.04**
		soil P	0.390 ± 0.04**
		plant P × soil P	0.397 ± 0.04**
	Twigs	control	0.323 ± 0.04**
		plant P	0.313 ± 0.04**
		soil P	0.325 ± 0.04**
		plant P × soil P	0.320 ± 0.04**

Notes: Values are means ± SE; $n = 3$.
† Control: no P fertilization, plant P: P-fertilized litter only, soil P: soil P-fertilized only, plant P × soil P: P-fertilized litter and soil P-fertilized.
* $P < 0.05$; ** $P < 0.01$.

Table 3.5. Initial litter chemistry.

Litter type	Treatment†	C ($mg \cdot g^{-1}$)	N ($mg \cdot g^{-1}$)	P ($mg \cdot g^{-1}$)	C:N (mass:mass)	C:P (mass:mass)	N:P (mass:mass)
Foliage	control	512.19 ± 2.56	15.45 ± 0.15	1.54 ± 0.21	33.17 ± 0.31	379.29 ± 58.61	11.41 ± 1.75
	plant P	508.71 ± 3.54	16.89 ± 0.34	8.51 ± 0.28	30.18 ± 0.59	60.29 ±2.07	2.00 ± 0.08
Roots	control	503.62 ± 2.95	9.86 ± 0.32	1.63 ± 0.20	51.39 ± 1.61	343.00 ± 45.18	6.73 ± 0.92
	plant P	488.80 ± 7.26	11.82 ± 0.58	3.54 ± 0.38	42.05 ± 2.37	149.71 ± 18.39	3.54 ± 0.38
Twigs	control	489.56 ± 2.60	7.95 ± 0.82	1.42 ± 0.12	66.54 ± 8.14	364.57 ± 39.25	5.60 ± 0.30
	plant P	488.61 ± 1.53	12.97 ± 1.23	4.03 ± 0.39	40.21 ± 4.62	130.86 ± 16.73	3.25 ± 0.14

Notes: Values are means ± SE; $n = 7$.

† Plant P: seedlings (litter source) fertilized with P.

CHAPTER 4:
CONCLUSION

This objective of this dissertation was to explore litter nutrient dynamics associated with the decomposition of multiple litter types in temperate coniferous forests with respect to differences in site, initial litter chemistry, and P availability. The use of ^{15}N-labelled litter revealed interesting N mineralization patterns that challenge traditional thoughts about N dynamics during decomposition. Although N was immobilized in the litter, this was still accompanied by net mineralization of N for all litter types and species. For leaf litter, these results are in stark contrast to the typical pattern of an N immobilization phase preceding N mineralization. Although this was a comparative study between litter types and species, the results for roots are of particular interest as this is the first study to use ^{15}N to examine N dynamics during fine root decomposition. Both the gross and net N mineralization results for roots from this study confirm that decomposing fine roots do undergo rapid mineralization of N in the early stages of decomposition and that patterns of N dynamics during fine root decomposition differ from patterns commonly observed in leaf litter. The results of this study also suggest that site environmental differences in these temperate coniferous forests are not as influential as initial chemistry with respect to decomposition rates and N dynamics.

The N mineralization patterns observed in the ^{15}N study indicate that litter has the potential to release substantial amounts of N to temperate coniferous forest systems on an annual basis in the early phases of decomposition and that these amounts may exceed other inputs of N to these systems. However, given the use of fresh litter in this study, the amounts of mineralized N observed in this study may

represent an upper bound of N mineralization, particularly for foliage, as this litter had higher N concentrations than those typically found in litterfall. Conversely, the rates of N mineralization observed in the ^{15}N study may realistically represent the amounts of N that may be released from slash remaining from logging operations. The patterns of N release also demonstrate that the temporal component of mineralization differs across litter types and species, as some litter types and species mineralized N more quickly than others. This may result in a "cascade" of N mineralization over time depending on the mix of litter and species present in a given system. While comparatively substantial amounts of N may be mineralized from decomposing litter, this study did not address the fate of the mineralized N. How tightly N is cycled in an ecosystem will determine whether the N that is mineralized during decomposition is retained or lost from the system.

The results from the P study demonstrate that relationships between soil P availability, litter P concentrations, decomposition, and litter nutrient dynamics in temperate coniferous forests are complex and vary with respect to different litter types. Initial litter nutrient concentrations seem to exert greater control over decomposition rates and litter nutrient dynamics during decomposition, although soil nutrient availability may also influence litter nutrient dynamics. Litter nutrient concentrations, nutrient mineralization patterns, and element ratios all responded to some degree to treatments with P-fertilized litter or soil. However, these responses were more indicative of N-limitation of decomposition rather than P-limitation. The rapid mineralization of P compared to the mineralization of N suggests that litter P was

contained in metabolically active pools that could be readily leached, but also that N was more limiting to decomposition than P, even in the control treatment.

The convergence of the specific element ratios to similar values across treatments within a given litter type in this study was quite striking given the large differences in initial litter nutrient concentrations between control and P-fertilized litter. This suggests that the element cycles of C, N, and P are similarly constrained and that N and P cycling may be closely coupled. These results also suggest that nutrient transformations during decomposition are regulated to maintain specific element ratios for a given pair of elements. Finally, this indicates that initial element ratios may predict litter nutrient dynamics during decomposition. This may be particularly true of N:P in terms of predicting P mineralization or immobilization given the evidence that N and P transformations during decomposition may be closely coupled.

The results of both of these studies suggest that initial litter chemistry exerts a strong influence over litter nutrient dynamics and that initial nutrient concentrations and element ratios may be important predictors of nutrient transformations during decomposition across multiple species and litter types. These transformations will have implications for fluxes of N and P within a forest ecosystem as well as fluxes between ecosystems as these elements cycle or recycle through the plant-soil continuum. Although understanding how individual elements cycle is important, this work emphasizes the importance of understanding how element cycles may be coupled. Coupled element cycling will have implications for ecosystem attributes such as nutrient availability, nutrient retention, nutrient loss, plant growth, and primary

productivity as plants and microbes both respond to and regulate nutrient flows and transformations. Thus, this work is fundamental to understanding how forest management practices may affect nutrient cycling but also to understanding how nutrient cycling may influence forest productivity in temperate coniferous forests.

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APPENDIX 1:
CHAPTER 2 SUPPLEMENTAL MATERIAL

Table A1.1. Analysis of variance (ANOVA) mixed effects models used for analyses.

Dependent variable	Fixed effects	Random effects	Repeated measures subject
Resin NH_4^+-N‡	Site, time, and site × time	Plot (site)	Plot × site × time
Resin NO^{3-}-N‡	Site, time, and site × time	Plot (site)	Plot × site × time
Resin PO_4^{2-}-P‡	Site, time, and site × time	Plot (site)	Plot × site × time
PMR*^	Site, species, litter, time, and all interactions	Plot (site)	Plot × site × species × time
PMR* $^+$	Site, species, litter, bag, time, and all interactions	Plot (site)	Plot × site × species × bag × time
F_{slow}†	Site, species, litter, and all interactions	Plot (site)	Plot × site × species
k_{slow}†	Site, species, litter, and all interactions	Plot (site)	Plot × site × species
F_{fast}†	Site, species, litter, and all interactions	Plot (site)	Plot × site × species
k_{fast}†	Site, species, litter, and all interactions	Plot (site)	Plot × site × species
Integrated k†	Site, species, litter, and all interactions	Plot (site)	Plot × site × species
k_e†	Site, species, litter, and all interactions	Plot (site)	Plot × site × species
Total N release†	Site, species, litter, and all interactions	Plot (site)	Plot × site × species
Total net N release†	Site, species, litter, and all interactions	Plot (site)	Plot × site × species
Total N uptake†	Site, species, litter, and all interactions	Plot (site)	Plot × site × species
Total N release per time interval^	Site, species, litter, time, and all interactions	Plot (site)	Plot × site × species × time
Net N release per time interval^	Site, species, litter, time, and all interactions	Plot (site)	Plot × site × species × time
N uptake per time interval^	Site, species, litter, time, and all interactions	Plot (site)	Plot × site × species × time

Notes: Dependent variables with the same symbol indicate the same model structure. The random effect plot (site) indicates plot was nested within site.

* PMR is percent initial litter mass remaining.

$^+$ This model was used for comparisons between mesh and cloth litterbags as well as mesh and buried mesh litterbags, where the fixed effect of "bag" was mesh and cloth or mesh and buried for each respective analysis.

Table A1.2. Ion exchange resin soil N and P availability at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Site	Collection date	Resin NH_4^+-N ($\mu g \cdot g^{-1}$ wet resin)	Resin NO_3^--N ($\mu g \cdot g^{-1}$ wet resin)	Resin PO_4^{3-}-P ($\mu g \cdot g^{-1}$ wet resin)
Cascade Head	August 2004	5.99 (- 0.89, + 1.27)**	0.213 ± 0.031**	4.97 (- 0.94, + 1.52)**
	November 2004	6.81 (- 1.01, + 1.45)**	0.250 ± 0.031**	60.33 (- 11.47, + 18.50)**
	February 2005	2.80 (- 0.42, + 0.59)**	0.256 ± 0.031**	10.96 (- 2.08, + 3.36)**
	May 2005	4.95 (- 0.74, + 1.05)**	0.278 ± 0.031**	11.64 (- 2.21, + 3.57)**
	August 2005	3.22 (- 0.49, + 0.70)**	0.000 ± 0.031	3.07 (- 0.59, + 0.97)**
	November 2005	4.38 (- 0.66, + 0.95)**	0.164 ± 0.031**	29.28 (- 5.66, + 9.23)**
	February 2006	7.48 (- 1.15, + 1.67)**	0.225 ± 0.031**	15.84 (- 3.12, + 5.16)**
	May 2006	4.85 (- 0.72, + 1.03)**	0.240 ± 0.031**	4.69 (- 0.89, + 1.44)**
	August 2006	10.45 (- 1.56, + 2.22)**	0.082 ± 0.031**	7.17 (- 1.36, + 2.20)**
	November 2006	7.73 (- 1.17, + 1.68)**	0.250 ± 0.031**	25.28 (- 4.89, + 7.97)**
H.J. Andrews	August 2004	5.65 (- 0.84, + 1.20)**	0.062 ± 0.031*	22.47 (- 4.27, + 6.89)**
	November 2004	6.16 (- 0.92, + 1.31)**	0.208 ± 0.031**	293.89 (- 55.86, + 90.11)**
	February 2005	3.10 (- 0.46, + 0.66)**	0.240 ± 0.031**	39.26 (- 7.46, + 12.04)**
	May 2005	2.60 (- 0.39, + 0.56)**	0.250 ± 0.031**	41.27 (- 7.84, + 12.66)**
	August 2005	5.33 (- 0.81, + 1.16)**	0.000 ± 0.031	19.02 (- 3.68, + 6.00)**
	November 2005	6.26 (- 0.93, + 1.33)**	0.162 ± 0.031**	193.55 (- 36.79, + 59.34) **
	February 2006	5.36 (- 0.81, + 1.16)**	0.250 ± 0.031**	69.42 (- 13.43, + 21.89)**
	May 2006	2.62 (- 0.39, + 0.56)**	0.245 ± 0.031**	21.86 (- 4.15, + 6.70)**
	August 2006	6.84 (- 1.02, + 1.45)**	0.295 ± 0.031**	33.51 (- 6.37, + 10.27)**
	November 2006	5.86 (- 0.87, + 1.25)**	0.192 ± 0.031**	71.15 (- 13.52, + 21.82)**

Notes: For NH_4^+-N and PO_4^{3-}-P values are back-transformed means (- lower SD, + upper SD). NO_3^--N values are means ± SE. For all three ions $n = 6$.
* $P < 0.05$; ** $P < 0.01$.

Table A1.3. Results from repeated measures ANOVA for mesh litterbag percent initial mass remaining (PMR) comparisons.

Dependent variable	Fixed effect	DF	F value	P
PMR	Site	1, 4	1.79	0.252
	Species	2, 241	5.30	**0.006**
	Litter	2, 241	188.53	**< 0.001**
	Time	6, 241	144.06	**< 0.001**
	Site × species	2, 241	0.04	0.959
	Site × litter	2, 241	9.80	**< 0.001**
	Site × time	6, 241	2.30	**0.035**
	Species × litter	4, 241	59.58	**< 0.001**
	Species × time	12, 241	0.97	0.479
	Time × litter	12, 241	2.31	**0.008**
	Site × species × time	12, 241	0.63	0.818
	Site × species × litter	4, 241	1.93	0.104
	Site × time × litter	12, 241	1.32	0.207
	Species × time × litter	24, 241	2.00	**0.005**
	Site × species × time × litter	24, 241	0.71	0.843

Notes: Boldface type denotes a significant effect ($P < 0.05$).

Table A1.4. Results from repeated measures ANOVA for mesh and cloth litterbag percent initial mass remaining (PMR) comparisons.

Dependent variable	Fixed effect	DF	F value	P
PMR	Site	1, 4	4.92	0.091
	Species	2, 210	18.61	**< 0.001**
	Litter	2, 210	170.20	**< 0.001**
	Bag	1, 210	50.74	**< 0.001**
	Time	2, 210	627.84	**< 0.001**
	Site × species	2, 210	0.20	0.823
	Site × litter	2, 210	1.42	0.244
	Site × bag	1, 210	1.12	0.291
	Site × time	2, 210	4.46	**0.013**
	Species × litter	4, 210	63.21	**< 0.001**
	Species × bag	2, 210	9.40	**0.001**
	Species × time	4, 210	7.81	**< 0.001**
	Time × bag	2, 210	3.72	**0.026**
	Time × litter	4, 210	2.06	0.087
	Litter × bag	2, 210	33.78	**< 0.001**
	Site × species × time	4, 210	1.35	0.251
	Site × species × litter	4, 210	2.74	**0.030**
	Site × species × bag	2, 210	0.40	0.669
	Site × time × litter	4, 210	1.00	0.409
	Site × time × bag	2, 210	0.60	0.551
	Site × litter × bag	2, 210	1.52	0.221
	Species × time × litter	8, 210	5.37	**< 0.001**
	Species × time × bag	4, 210	19.14	**< 0.001**
	Species × bag × litter	4, 210	0.58	0.676
	Time × bag × litter	4, 210	1.69	0.154
	Site × species × litter × time	8, 210	1.21	0.295
	Site × species × litter × bag	4, 210	1.35	0.253
	Site × species × time × bag	4, 210	0.74	0.566
	Site × litter × time × bag	4, 210	1.82	0.127
	Species × litter × time × bag	8, 210	2.62	**0.010**
	Site × species × litter × time × bag	8, 210	0.75	0.648

Notes: Boldface type denotes a significant effect ($P < 0.05$).

Table A1.5. Results from repeated measures ANOVA for mesh and buried mesh litterbag percent initial mass remaining (PMR) comparisons.

Dependent variable	Fixed effect	DF	F value	P
PMR	Site	1, 4	2.17	0.215
	Species	1, 90	27.36	**< 0.001**
	Litter	1, 90	135.67	**< 0.001**
	Bag	1, 90	330.44	**< 0.001**
	Time	2, 90	598.74	**< 0.001**
	Site × species	1, 90	1.30	0.256
	Site × litter	1, 90	1.10	0.297
	Site × bag	1, 90	3.24	0.075
	Site × time	2, 90	5.03	**0.009**
	Species × litter	1, 90	141.13	**< 0.001**
	Species × bag	1, 90	0.67	0.416
	Species × time	2, 90	7.81	**< 0.001**
	Time × bag	2, 90	8.67	**< 0.001**
	Time × litter	2, 90	1.98	0.144
	Litter × bag	1, 90	4.98	**0.028**
	Site × species × time	2, 90	0.82	0.445
	Site × species × litter	1, 90	1.60	0.210
	Site × species × bag	1, 90	0.46	0.501
	Site × time× litter	2, 90	0.02	0.981
	Site × time × bag	2, 90	1.13	0.328
	Site × litter × bag	1, 90	0.01	0.916
	Species × time × litter	2, 90	3.84	**0.025**
	Species × time × bag	2, 90	3.34	**0.040**
	Species × bag × litter	1, 90	2.26	0.136
	Time × bag × litter	2, 90	4.72	**0.011**
	Site × species × litter × time	2, 90	1.01	0.370
	Site × species × litter × bag	1, 90	0.56	0.455
	Site × species × time × bag	2, 90	2.97	0.057
	Site × litter × time × bag	2, 90	1.98	0.144
	Species × litter × time × bag	2, 90	6.15	**0.003**
	Site × species × litter time × bag	2, 90	0.86	0.425

Notes: Boldface type denotes a significant effect ($P < 0.05$).

Table A1.6. Pairwise comparisons of site × litter × species combinations for integrated *k* values for litter decomposition in mesh litterbags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
Cascade Head	bigleaf maple	foliage	Cascade Head	bigleaf maple	roots	0.95
Cascade Head	bigleaf maple	foliage	Cascade Head	bigleaf maple	twigs	1.00
Cascade Head	bigleaf maple	foliage	Cascade Head	Sitka spruce	foliage	0.99
Cascade Head	bigleaf maple	foliage	Cascade Head	Sitka spruce	roots	1.00
Cascade Head	bigleaf maple	foliage	Cascade Head	Sitka spruce	twigs	1.00
Cascade Head	bigleaf maple	foliage	Cascade Head	Douglas-fir	foliage	1.00
Cascade Head	bigleaf maple	foliage	Cascade Head	Douglas-fir	roots	1.00
Cascade Head	bigleaf maple	foliage	Cascade Head	Douglas-fir	twigs	1.00
Cascade Head	bigleaf maple	foliage	H. J. Andrews	bigleaf maple	foliage	1.00
Cascade Head	bigleaf maple	foliage	H. J. Andrews	bigleaf maple	roots	0.97
Cascade Head	bigleaf maple	foliage	H. J. Andrews	bigleaf maple	twigs	1.00
Cascade Head	bigleaf maple	foliage	H. J. Andrews	Sitka spruce	foliage	0.97
Cascade Head	bigleaf maple	foliage	H. J. Andrews	Sitka spruce	roots	1.00
Cascade Head	bigleaf maple	foliage	H. J. Andrews	Sitka spruce	twigs	1.00
Cascade Head	bigleaf maple	foliage	H. J. Andrews	Douglas-fir	foliage	1.00
Cascade Head	bigleaf maple	foliage	H. J. Andrews	Douglas-fir	roots	1.00
Cascade Head	bigleaf maple	foliage	H. J. Andrews	Douglas-fir	twigs	1.00
Cascade Head	bigleaf maple	roots	Cascade Head	bigleaf maple	twigs	0.99
Cascade Head	bigleaf maple	roots	Cascade Head	Sitka spruce	foliage	1.00
Cascade Head	bigleaf maple	roots	Cascade Head	Sitka spruce	roots	0.80
Cascade Head	bigleaf maple	roots	Cascade Head	Sitka spruce	twigs	0.12
Cascade Head	bigleaf maple	roots	Cascade Head	Douglas-fir	foliage	1.00

Notes: Boldface type denotes a significant ($P < 0.05$) difference.

Table A1.6. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
Cascade Head	bigleaf maple	roots	Cascade Head	Douglas-fir	roots	0.08
Cascade Head	bigleaf maple	roots	Cascade Head	Douglas-fir	twigs	0.55
Cascade Head	bigleaf maple	roots	H. J. Andrews	bigleaf maple	foliage	1.00
Cascade Head	bigleaf maple	roots	H. J. Andrews	bigleaf maple	roots	1.00
Cascade Head	bigleaf maple	roots	H. J. Andrews	bigleaf maple	twigs	1.00
Cascade Head	bigleaf maple	roots	H. J. Andrews	Sitka spruce	foliage	1.00
Cascade Head	bigleaf maple	roots	H. J. Andrews	Sitka spruce	roots	1.00
Cascade Head	bigleaf maple	roots	H. J. Andrews	Sitka spruce	twigs	0.16
Cascade Head	bigleaf maple	roots	H. J. Andrews	Douglas-fir	foliage	1.00
Cascade Head	bigleaf maple	roots	H. J. Andrews	Douglas-fir	roots	0.87
Cascade Head	bigleaf maple	roots	H. J. Andrews	Douglas-fir	twigs	0.94
Cascade Head	bigleaf maple	twigs	Cascade Head	Sitka spruce	foliage	1.00
Cascade Head	bigleaf maple	twigs	Cascade Head	Sitka spruce	roots	1.00
Cascade Head	bigleaf maple	twigs	Cascade Head	Sitka spruce	twigs	0.98
Cascade Head	bigleaf maple	twigs	Cascade Head	Douglas-fir	foliage	1.00
Cascade Head	bigleaf maple	twigs	Cascade Head	Douglas-fir	roots	0.95
Cascade Head	bigleaf maple	twigs	Cascade Head	Douglas-fir	twigs	1.00
Cascade Head	bigleaf maple	twigs	H. J. Andrews	bigleaf maple	foliage	1.00
Cascade Head	bigleaf maple	twigs	H. J. Andrews	bigleaf maple	roots	0.96
Cascade Head	bigleaf maple	twigs	H. J. Andrews	bigleaf maple	twigs	1.00
Cascade Head	bigleaf maple	twigs	H. J. Andrews	Sitka spruce	foliage	1.00
Cascade Head	bigleaf maple	twigs	H. J. Andrews	Sitka spruce	roots	1.00
Cascade Head	bigleaf maple	twigs	H. J. Andrews	Sitka spruce	twigs	0.96
Cascade Head	bigleaf maple	twigs	H. J. Andrews	Douglas-fir	foliage	1.00

Table A1.6. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
Cascade Head	bigleaf maple	twigs	H. J. Andrews	Douglas-fir	roots	1.00
Cascade Head	bigleaf maple	twigs	H. J. Andrews	Douglas-fir	twigs	1.00
Cascade Head	Sitka spruce	foliage	Cascade Head	Sitka spruce	roots	1.00
Cascade Head	Sitka spruce	foliage	Cascade Head	Sitka spruce	twigs	0.96
Cascade Head	Sitka spruce	foliage	Cascade Head	Douglas-fir	foliage	1.00
Cascade Head	Sitka spruce	foliage	Cascade Head	Douglas-fir	roots	0.94
Cascade Head	Sitka spruce	foliage	Cascade Head	Douglas-fir	twigs	1.00
Cascade Head	Sitka spruce	foliage	H. J. Andrews	bigleaf maple	foliage	1.00
Cascade Head	Sitka spruce	foliage	H. J. Andrews	bigleaf maple	roots	1.00
Cascade Head	Sitka spruce	foliage	H. J. Andrews	bigleaf maple	twigs	1.00
Cascade Head	Sitka spruce	foliage	H. J. Andrews	Sitka spruce	foliage	1.00
Cascade Head	Sitka spruce	foliage	H. J. Andrews	Sitka spruce	roots	1.00
Cascade Head	Sitka spruce	foliage	H. J. Andrews	Sitka spruce	twigs	0.92
Cascade Head	Sitka spruce	foliage	H. J. Andrews	Douglas-fir	foliage	1.00
Cascade Head	Sitka spruce	foliage	H. J. Andrews	Douglas-fir	roots	1.00
Cascade Head	Sitka spruce	foliage	H. J. Andrews	Douglas-fir	twigs	1.00
Cascade Head	Sitka spruce	roots	Cascade Head	Sitka spruce	twigs	1.00
Cascade Head	Sitka spruce	roots	Cascade Head	Douglas-fir	foliage	1.00
Cascade Head	Sitka spruce	roots	Cascade Head	Douglas-fir	roots	0.99
Cascade Head	Sitka spruce	roots	Cascade Head	Douglas-fir	twigs	1.00
Cascade Head	Sitka spruce	roots	H. J. Andrews	bigleaf maple	foliage	1.00
Cascade Head	Sitka spruce	roots	H. J. Andrews	bigleaf maple	roots	0.92
Cascade Head	Sitka spruce	roots	H. J. Andrews	bigleaf maple	twigs	1.00
Cascade Head	Sitka spruce	roots	H. J. Andrews	Sitka spruce	foliage	0.99

Table A1.6. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
Cascade Head	Sitka spruce	roots	H. J. Andrews	Sitka spruce	roots	1.00
Cascade Head	Sitka spruce	roots	H. J. Andrews	Sitka spruce	twigs	0.99
Cascade Head	Sitka spruce	roots	H. J. Andrews	Douglas-fir	foliage	1.00
Cascade Head	Sitka spruce	roots	H. J. Andrews	Douglas-fir	roots	1.00
Cascade Head	Sitka spruce	roots	H. J. Andrews	Douglas-fir	twigs	1.00
Cascade Head	Sitka spruce	twigs	Cascade Head	Douglas-fir	foliage	1.00
Cascade Head	Sitka spruce	twigs	Cascade Head	Douglas-fir	roots	1.00
Cascade Head	Sitka spruce	twigs	Cascade Head	Douglas-fir	twigs	1.00
Cascade Head	Sitka spruce	twigs	H. J. Andrews	bigleaf maple	foliage	1.00
Cascade Head	Sitka spruce	twigs	H. J. Andrews	bigleaf maple	roots	0.31
Cascade Head	Sitka spruce	twigs	H. J. Andrews	bigleaf maple	twigs	0.66
Cascade Head	Sitka spruce	twigs	H. J. Andrews	Sitka spruce	foliage	0.89
Cascade Head	Sitka spruce	twigs	H. J. Andrews	Sitka spruce	roots	0.90
Cascade Head	Sitka spruce	twigs	H. J. Andrews	Sitka spruce	twigs	1.00
Cascade Head	Sitka spruce	twigs	H. J. Andrews	Douglas-fir	foliage	0.99
Cascade Head	Sitka spruce	twigs	H. J. Andrews	Douglas-fir	roots	1.00
Cascade Head	Sitka spruce	twigs	H. J. Andrews	Douglas-fir	twigs	1.00
Cascade Head	Douglas-fir	foliage	Cascade Head	Douglas-fir	roots	1.00
Cascade Head	Douglas-fir	foliage	Cascade Head	Douglas-fir	twigs	1.00
Cascade Head	Douglas-fir	foliage	H. J. Andrews	bigleaf maple	foliage	1.00
Cascade Head	Douglas-fir	foliage	H. J. Andrews	bigleaf maple	roots	1.00
Cascade Head	Douglas-fir	foliage	H. J. Andrews	bigleaf maple	twigs	1.00
Cascade Head	Douglas-fir	foliage	H. J. Andrews	Sitka spruce	foliage	1.00
Cascade Head	Douglas-fir	foliage	H. J. Andrews	Sitka spruce	roots	1.00

Table A1.6. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
Cascade Head	Douglas-fir	foliage	H. J. Andrews	Sitka spruce	twigs	1.00
Cascade Head	Douglas-fir	foliage	H. J. Andrews	Douglas-fir	foliage	1.00
Cascade Head	Douglas-fir	foliage	H. J. Andrews	Douglas-fir	roots	1.00
Cascade Head	Douglas-fir	foliage	H. J. Andrews	Douglas-fir	twigs	1.00
Cascade Head	Douglas-fir	roots	Cascade Head	Douglas-fir	twigs	1.00
Cascade Head	Douglas-fir	roots	H. J. Andrews	bigleaf maple	foliage	1.00
Cascade Head	Douglas-fir	roots	H. J. Andrews	bigleaf maple	roots	0.23
Cascade Head	Douglas-fir	roots	H. J. Andrews	bigleaf maple	twigs	0.54
Cascade Head	Douglas-fir	roots	H. J. Andrews	Sitka spruce	foliage	0.85
Cascade Head	Douglas-fir	roots	H. J. Andrews	Sitka spruce	roots	0.82
Cascade Head	Douglas-fir	roots	H. J. Andrews	Sitka spruce	twigs	1.00
Cascade Head	Douglas-fir	roots	H. J. Andrews	Douglas-fir	foliage	0.98
Cascade Head	Douglas-fir	roots	H. J. Andrews	Douglas-fir	roots	1.00
Cascade Head	Douglas-fir	roots	H. J. Andrews	Douglas-fir	twigs	1.00
Cascade Head	Douglas-fir	twigs	H. J. Andrews	bigleaf maple	foliage	1.00
Cascade Head	Douglas-fir	twigs	H. J. Andrews	bigleaf maple	roots	0.78
Cascade Head	Douglas-fir	twigs	H. J. Andrews	bigleaf maple	twigs	0.98
Cascade Head	Douglas-fir	twigs	H. J. Andrews	Sitka spruce	foliage	0.98
Cascade Head	Douglas-fir	twigs	H. J. Andrews	Sitka spruce	roots	1.00
Cascade Head	Douglas-fir	twigs	H. J. Andrews	Sitka spruce	twigs	1.00
Cascade Head	Douglas-fir	twigs	H. J. Andrews	Douglas-fir	foliage	1.00
Cascade Head	Douglas-fir	twigs	H. J. Andrews	Douglas-fir	roots	1.00
Cascade Head	Douglas-fir	twigs	H. J. Andrews	Douglas-fir	twigs	1.00
H. J. Andrews	bigleaf maple	foliage	H. J. Andrews	bigleaf maple	roots	1.00

Table A1.6. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
H. J. Andrews	bigleaf maple	foliage	H. J. Andrews	bigleaf maple	twigs	1.00
H. J. Andrews	bigleaf maple	foliage	H. J. Andrews	Sitka spruce	foliage	1.00
H. J. Andrews	bigleaf maple	foliage	H. J. Andrews	Sitka spruce	roots	1.00
H. J. Andrews	bigleaf maple	foliage	H. J. Andrews	Sitka spruce	twigs	1.00
H. J. Andrews	bigleaf maple	foliage	H. J. Andrews	Douglas-fir	foliage	1.00
H. J. Andrews	bigleaf maple	foliage	H. J. Andrews	Douglas-fir	roots	1.00
H. J. Andrews	bigleaf maple	foliage	H. J. Andrews	Douglas-fir	twigs	1.00
H. J. Andrews	bigleaf maple	roots	H. J. Andrews	bigleaf maple	twigs	1.00
H. J. Andrews	bigleaf maple	roots	H. J. Andrews	Sitka spruce	foliage	1.00
H. J. Andrews	bigleaf maple	roots	H. J. Andrews	Sitka spruce	roots	1.00
H. J. Andrews	bigleaf maple	roots	H. J. Andrews	Sitka spruce	twigs	**0.03**
H. J. Andrews	bigleaf maple	roots	H. J. Andrews	Douglas-fir	foliage	1.00
H. J. Andrews	bigleaf maple	roots	H. J. Andrews	Douglas-fir	roots	0.62
H. J. Andrews	bigleaf maple	roots	H. J. Andrews	Douglas-fir	twigs	0.75
H. J. Andrews	bigleaf maple	twigs	H. J. Andrews	Sitka spruce	foliage	1.00
H. J. Andrews	bigleaf maple	twigs	H. J. Andrews	Sitka spruce	roots	1.00
H. J. Andrews	bigleaf maple	twigs	H. J. Andrews	Sitka spruce	twigs	0.13
H. J. Andrews	bigleaf maple	twigs	H. J. Andrews	Douglas-fir	foliage	1.00
H. J. Andrews	bigleaf maple	twigs	H. J. Andrews	Douglas-fir	roots	0.95
H. J. Andrews	bigleaf maple	twigs	H. J. Andrews	Douglas-fir	twigs	0.98
H. J. Andrews	Sitka spruce	foliage	H. J. Andrews	Sitka spruce	roots	1.00
H. J. Andrews	Sitka spruce	foliage	H. J. Andrews	Sitka spruce	twigs	0.76
H. J. Andrews	Sitka spruce	foliage	H. J. Andrews	Douglas-fir	foliage	1.00
H. J. Andrews	Sitka spruce	foliage	H. J. Andrews	Douglas-fir	roots	0.98

Table A1.6. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
H. J. Andrews	Sitka spruce	foliage	H. J. Andrews	Douglas-fir	twigs	0.99
H. J. Andrews	Sitka spruce	roots	H. J. Andrews	Sitka spruce	twigs	0.79
H. J. Andrews	Sitka spruce	roots	H. J. Andrews	Douglas-fir	foliage	1.00
H. J. Andrews	Sitka spruce	roots	H. J. Andrews	Douglas-fir	roots	1.00
H. J. Andrews	Sitka spruce	roots	H. J. Andrews	Douglas-fir	twigs	1.00
H. J. Andrews	Sitka spruce	twigs	H. J. Andrews	Douglas-fir	foliage	0.95
H. J. Andrews	Sitka spruce	twigs	H. J. Andrews	Douglas-fir	roots	0.98
H. J. Andrews	Sitka spruce	twigs	H. J. Andrews	Douglas-fir	twigs	0.92
H. J. Andrews	Douglas-fir	foliage	H. J. Andrews	Douglas-fir	roots	1.00
H. J. Andrews	Douglas-fir	foliage	H. J. Andrews	Douglas-fir	twigs	1.00
H. J. Andrews	Douglas-fir	roots	H. J. Andrews	Douglas-fir	twigs	1.00

Table A1.7. Pairwise comparisons of site × litter × species combinations for k_e values for 2.5 years of litter decomposition in mesh litterbags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
Cascade Head	foliage	bigleaf maple	Cascade Head	roots	bigleaf maple	0.199
Cascade Head	foliage	bigleaf maple	Cascade Head	twigs	bigleaf maple	0.973
Cascade Head	foliage	bigleaf maple	Cascade Head	foliage	Sitka spruce	**< 0.001**
Cascade Head	foliage	bigleaf maple	Cascade Head	roots	Sitka spruce	0.634
Cascade Head	foliage	bigleaf maple	Cascade Head	twigs	Sitka spruce	0.988
Cascade Head	foliage	bigleaf maple	Cascade Head	foliage	Douglas-fir	**0.001**
Cascade Head	foliage	bigleaf maple	Cascade Head	roots	Douglas-fir	1.000
Cascade Head	foliage	bigleaf maple	Cascade Head	twigs	Douglas-fir	1.000
Cascade Head	foliage	bigleaf maple	H. J. Andrews	foliage	bigleaf maple	0.999
Cascade Head	foliage	bigleaf maple	H. J. Andrews	roots	bigleaf maple	**0.007**
Cascade Head	foliage	bigleaf maple	H. J. Andrews	twigs	bigleaf maple	1.000
Cascade Head	foliage	bigleaf maple	H. J. Andrews	foliage	Sitka spruce	**0.001**
Cascade Head	foliage	bigleaf maple	H. J. Andrews	roots	Sitka spruce	0.602
Cascade Head	foliage	bigleaf maple	H. J. Andrews	twigs	Sitka spruce	0.744
Cascade Head	foliage	bigleaf maple	H. J. Andrews	foliage	Douglas-fir	**0.005**
Cascade Head	foliage	bigleaf maple	H. J. Andrews	roots	Douglas-fir	0.662
Cascade Head	foliage	bigleaf maple	H. J. Andrews	twigs	Douglas-fir	1.000
Cascade Head	roots	bigleaf maple	Cascade Head	twigs	bigleaf maple	0.732
Cascade Head	roots	bigleaf maple	Cascade Head	foliage	Sitka spruce	0.164
Cascade Head	roots	bigleaf maple	Cascade Head	roots	Sitka spruce	1.000
Cascade Head	roots	bigleaf maple	Cascade Head	twigs	Sitka spruce	**< 0.001**
Cascade Head	roots	bigleaf maple	Cascade Head	foliage	Douglas-fir	0.603

Notes: Boldface type denotes a significant ($P < 0.05$) difference.

Table A1.7. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
Cascade Head	roots	bigleaf maple	Cascade Head	roots	Douglas-fir	0.676
Cascade Head	roots	bigleaf maple	Cascade Head	twigs	Douglas-fir	0.107
Cascade Head	roots	bigleaf maple	H. J. Andrews	foliage	bigleaf maple	0.892
Cascade Head	roots	bigleaf maple	H. J. Andrews	roots	bigleaf maple	0.976
Cascade Head	roots	bigleaf maple	H. J. Andrews	twigs	bigleaf maple	**0.002**
Cascade Head	roots	bigleaf maple	H. J. Andrews	foliage	Sitka spruce	0.481
Cascade Head	roots	bigleaf maple	H. J. Andrews	roots	Sitka spruce	1.000
Cascade Head	roots	bigleaf maple	H. J. Andrews	twigs	Sitka spruce	**< 0.001**
Cascade Head	roots	bigleaf maple	H. J. Andrews	foliage	Douglas-fir	0.893
Cascade Head	roots	bigleaf maple	H. J. Andrews	roots	Douglas-fir	1.000
Cascade Head	roots	bigleaf maple	H. J. Andrews	twigs	Douglas-fir	**0.010**
Cascade Head	twigs	bigleaf maple	Cascade Head	foliage	Sitka spruce	**< 0.001**
Cascade Head	twigs	bigleaf maple	Cascade Head	roots	Sitka spruce	0.999
Cascade Head	twigs	bigleaf maple	Cascade Head	twigs	Sitka spruce	**< 0.001**
Cascade Head	twigs	bigleaf maple	Cascade Head	foliage	Douglas-fir	**0.002**
Cascade Head	twigs	bigleaf maple	Cascade Head	roots	Douglas-fir	1.000
Cascade Head	twigs	bigleaf maple	Cascade Head	twigs	Douglas-fir	0.786
Cascade Head	twigs	bigleaf maple	H. J. Andrews	foliage	bigleaf maple	1.000
Cascade Head	twigs	bigleaf maple	H. J. Andrews	roots	bigleaf maple	**0.017**
Cascade Head	twigs	bigleaf maple	H. J. Andrews	twigs	bigleaf maple	**0.004**
Cascade Head	twigs	bigleaf maple	H. J. Andrews	foliage	Sitka spruce	**0.001**
Cascade Head	twigs	bigleaf maple	H. J. Andrews	roots	Sitka spruce	0.998
Cascade Head	twigs	bigleaf maple	H. J. Andrews	twigs	Sitka spruce	**< 0.001**
Cascade Head	twigs	bigleaf maple	H. J. Andrews	foliage	Douglas-fir	**0.014**

Table A1.7. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
Cascade Head	twigs	bigleaf maple	H. J. Andrews	roots	Douglas-fir	1.000
Cascade Head	twigs	bigleaf maple	H. J. Andrews	twigs	Douglas-fir	0.051
Cascade Head	foliage	Sitka spruce	Cascade Head	roots	Sitka spruce	**0.030**
Cascade Head	foliage	Sitka spruce	Cascade Head	twigs	Sitka spruce	**< 0.001**
Cascade Head	foliage	Sitka spruce	Cascade Head	foliage	Douglas-fir	1.000
Cascade Head	foliage	Sitka spruce	Cascade Head	roots	Douglas-fir	**0.001**
Cascade Head	foliage	Sitka spruce	Cascade Head	twigs	Douglas-fir	**< 0.001**
Cascade Head	foliage	Sitka spruce	H. J. Andrews	foliage	bigleaf maple	**0.004**
Cascade Head	foliage	Sitka spruce	H. J. Andrews	roots	bigleaf maple	0.948
Cascade Head	foliage	Sitka spruce	H. J. Andrews	twigs	bigleaf maple	**< 0.001**
Cascade Head	foliage	Sitka spruce	H. J. Andrews	foliage	Sitka spruce	1.000
Cascade Head	foliage	Sitka spruce	H. J. Andrews	roots	Sitka spruce	**0.038**
Cascade Head	foliage	Sitka spruce	H. J. Andrews	twigs	Sitka spruce	**< 0.001**
Cascade Head	foliage	Sitka spruce	H. J. Andrews	foliage	Douglas-fir	0.998
Cascade Head	foliage	Sitka spruce	H. J. Andrews	roots	Douglas-fir	**0.031**
Cascade Head	foliage	Sitka spruce	H. J. Andrews	twigs	Douglas-fir	**< 0.001**
Cascade Head	roots	Sitka spruce	Cascade Head	twigs	Sitka spruce	**0.003**
Cascade Head	roots	Sitka spruce	Cascade Head	foliage	Douglas-fir	0.166
Cascade Head	roots	Sitka spruce	Cascade Head	roots	Douglas-fir	0.991
Cascade Head	roots	Sitka spruce	Cascade Head	twigs	Douglas-fir	0.681
Cascade Head	roots	Sitka spruce	H. J. Andrews	foliage	bigleaf maple	1.000
Cascade Head	roots	Sitka spruce	H. J. Andrews	roots	bigleaf maple	0.589
Cascade Head	roots	Sitka spruce	H. J. Andrews	twigs	bigleaf maple	**0.035**

Table A1.7. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
Cascade Head	roots	Sitka spruce	H. J. Andrews	foliage	Sitka spruce	0.117
Cascade Head	roots	Sitka spruce	H. J. Andrews	roots	Sitka spruce	1.000
Cascade Head	roots	Sitka spruce	H. J. Andrews	twigs	Sitka spruce	**< 0.001**
Cascade Head	roots	Sitka spruce	H. J. Andrews	foliage	Douglas-fir	0.417
Cascade Head	roots	Sitka spruce	H. J. Andrews	roots	Douglas-fir	1.000
Cascade Head	roots	Sitka spruce	H. J. Andrews	twigs	Douglas-fir	0.139
Cascade Head	twigs	Sitka spruce	Cascade Head	foliage	Douglas-fir	**< 0.001**
Cascade Head	twigs	Sitka spruce	Cascade Head	roots	Douglas-fir	0.207
Cascade Head	twigs	Sitka spruce	Cascade Head	twigs	Douglas-fir	**0.003**
Cascade Head	twigs	Sitka spruce	H. J. Andrews	foliage	bigleaf maple	0.289
Cascade Head	twigs	Sitka spruce	H. J. Andrews	roots	bigleaf maple	**< 0.001**
Cascade Head	twigs	Sitka spruce	H. J. Andrews	twigs	bigleaf maple	0.988
Cascade Head	twigs	Sitka spruce	H. J. Andrews	foliage	Sitka spruce	**< 0.001**
Cascade Head	twigs	Sitka spruce	H. J. Andrews	roots	Sitka spruce	**0.003**
Cascade Head	twigs	Sitka spruce	H. J. Andrews	twigs	Sitka spruce	0.987
Cascade Head	twigs	Sitka spruce	H. J. Andrews	foliage	Douglas-fir	**< 0.001**
Cascade Head	twigs	Sitka spruce	H. J. Andrews	roots	Douglas-fir	**0.004**
Cascade Head	twigs	Sitka spruce	H. J. Andrews	twigs	Douglas-fir	0.552
Cascade Head	foliage	Douglas-fir	Cascade Head	roots	Douglas-fir	**0.009**
Cascade Head	foliage	Douglas-fir	Cascade Head	twigs	Douglas-fir	**0.003**
Cascade Head	foliage	Douglas-fir	H. J. Andrews	foliage	bigleaf maple	**0.029**
Cascade Head	foliage	Douglas-fir	H. J. Andrews	roots	bigleaf maple	1.000
Cascade Head	foliage	Douglas-fir	H. J. Andrews	twigs	bigleaf maple	**< 0.001**
Cascade Head	foliage	Douglas-fir	H. J. Andrews	foliage	Sitka spruce	1.000
Cascade Head	foliage	Douglas-fir	H. J. Andrews	roots	Sitka spruce	0.222

Table A1.7. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
Cascade Head	foliage	Douglas-fir	H. J. Andrews	twigs	Sitka spruce	**< 0.001**
Cascade Head	foliage	Douglas-fir	H. J. Andrews	foliage	Douglas-fir	1.000
Cascade Head	foliage	Douglas-fir	H. J. Andrews	roots	Douglas-fir	0.186
Cascade Head	foliage	Douglas-fir	H. J. Andrews	twigs	Douglas-fir	**< 0.001**
Cascade Head	roots	Douglas-fir	Cascade Head	twigs	Douglas-fir	1.000
Cascade Head	roots	Douglas-fir	H. J. Andrews	foliage	bigleaf maple	1.000
Cascade Head	roots	Douglas-fir	H. J. Andrews	roots	bigleaf maple	**0.045**
Cascade Head	roots	Douglas-fir	H. J. Andrews	twigs	bigleaf maple	0.772
Cascade Head	roots	Douglas-fir	H. J. Andrews	foliage	Sitka spruce	**0.005**
Cascade Head	roots	Douglas-fir	H. J. Andrews	roots	Sitka spruce	0.985
Cascade Head	roots	Douglas-fir	H. J. Andrews	twigs	Sitka spruce	**0.040**
Cascade Head	roots	Douglas-fir	H. J. Andrews	foliage	Douglas-fir	**0.030**
Cascade Head	roots	Douglas-fir	H. J. Andrews	roots	Douglas-fir	0.993
Cascade Head	roots	Douglas-fir	H. J. Andrews	twigs	Douglas-fir	0.980
Cascade Head	twigs	Douglas-fir	H. J. Andrews	foliage	bigleaf maple	1.000
Cascade Head	twigs	Douglas-fir	H. J. Andrews	roots	bigleaf maple	**0.001**
Cascade Head	twigs	Douglas-fir	H. J. Andrews	twigs	bigleaf maple	0.307
Cascade Head	twigs	Douglas-fir	H. J. Andrews	foliage	Sitka spruce	**< 0.001**
Cascade Head	twigs	Douglas-fir	H. J. Andrews	roots	Sitka spruce	0.651
Cascade Head	twigs	Douglas-fir	H. J. Andrews	twigs	Sitka spruce	**< 0.001**
Cascade Head	twigs	Douglas-fir	H. J. Andrews	foliage	Douglas-fir	**0.001**
Cascade Head	twigs	Douglas-fir	H. J. Andrews	roots	Douglas-fir	0.731
Cascade Head	twigs	Douglas-fir	H. J. Andrews	twigs	Douglas-fir	0.903
H. J. Andrews	foliage	bigleaf maple	H. J. Andrews	roots	bigleaf maple	0.125

Table A1.7. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
H. J. Andrews	foliage	bigleaf maple	H. J. Andrews	twigs	bigleaf maple	0.922
H. J. Andrews	foliage	bigleaf maple	H. J. Andrews	foliage	Sitka spruce	**0.014**
H. J. Andrews	foliage	bigleaf maple	H. J. Andrews	roots	Sitka spruce	0.998
H. J. Andrews	foliage	bigleaf maple	H. J. Andrews	twigs	Sitka spruce	**0.047**
H. J. Andrews	foliage	bigleaf maple	H. J. Andrews	foliage	Douglas-fir	0.073
H. J. Andrews	foliage	bigleaf maple	H. J. Andrews	roots	Douglas-fir	0.999
H. J. Andrews	foliage	bigleaf maple	H. J. Andrews	twigs	Douglas-fir	0.961
H. J. Andrews	roots	bigleaf maple	H. J. Andrews	twigs	bigleaf maple	**< 0.001**
H. J. Andrews	roots	bigleaf maple	H. J. Andrews	foliage	Sitka spruce	0.999
H. J. Andrews	roots	bigleaf maple	H. J. Andrews	roots	Sitka spruce	0.621
H. J. Andrews	roots	bigleaf maple	H. J. Andrews	twigs	Sitka spruce	**< 0.001**
H. J. Andrews	roots	bigleaf maple	H. J. Andrews	foliage	Douglas-fir	1.000
H. J. Andrews	roots	bigleaf maple	H. J. Andrews	roots	Douglas-fir	0.555
H. J. Andrews	roots	bigleaf maple	H. J. Andrews	twigs	Douglas-fir	**< 0.001**
H. J. Andrews	twigs	bigleaf maple	H. J. Andrews	foliage	Sitka spruce	**< 0.001**
H. J. Andrews	twigs	bigleaf maple	H. J. Andrews	roots	Sitka spruce	**0.018**
H. J. Andrews	twigs	bigleaf maple	H. J. Andrews	twigs	Sitka spruce	0.157
H. J. Andrews	twigs	bigleaf maple	H. J. Andrews	foliage	Douglas-fir	**< 0.001**
H. J. Andrews	twigs	bigleaf maple	H. J. Andrews	roots	Douglas-fir	**0.025**
H. J. Andrews	twigs	bigleaf maple	H. J. Andrews	twigs	Douglas-fir	0.999
H. J. Andrews	foliage	Sitka spruce	H. J. Andrews	roots	Sitka spruce	0.138
H. J. Andrews	foliage	Sitka spruce	H. J. Andrews	twigs	Sitka spruce	**< 0.001**
H. J. Andrews	foliage	Sitka spruce	H. J. Andrews	foliage	Douglas-fir	1.000
H. J. Andrews	foliage	Sitka spruce	H. J. Andrews	roots	Douglas-fir	0.102

Table A1.7. Continued.

Site 1	Litter type 1	Species 1	Site 2	Litter type 2	Species 2	P
H. J. Andrews	foliage	Sitka spruce	H. J. Andrews	twigs	Douglas-fir	**< 0.001**
H. J. Andrews	roots	Sitka spruce	H. J. Andrews	twigs	Sitka spruce	**< 0.001**
H. J. Andrews	roots	Sitka spruce	H. J. Andrews	foliage	Douglas-fir	0.444
H. J. Andrews	roots	Sitka spruce	H. J. Andrews	roots	Douglas-fir	1.000
H. J. Andrews	roots	Sitka spruce	H. J. Andrews	twigs	Douglas-fir	0.081
H. J. Andrews	twigs	Sitka spruce	H. J. Andrews	foliage	Douglas-fir	**< 0.001**
H. J. Andrews	twigs	Sitka spruce	H. J. Andrews	roots	Douglas-fir	**< 0.001**
H. J. Andrews	twigs	Sitka spruce	H. J. Andrews	twigs	Douglas-fir	**0.011**
H. J. Andrews	foliage	Douglas-fir	H. J. Andrews	roots	Douglas-fir	0.411
H. J. Andrews	foliage	Douglas-fir	H. J. Andrews	twigs	Douglas-fir	**0.001**
H. J. Andrews	roots	Douglas-fir	H. J. Andrews	twigs	Douglas-fir	0.133

Table A1.8. Results from repeated measures ANOVA for N release and uptake for 2.5 years of litter decomposition in mesh litterbags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Dependent variable	Fixed effect	DF	F value	P
Gross N release	Site	1, 4	0.27	0.629
	Species	2, 31	5.79	**0.007**
	Litter	2, 31	6.24	**0.005**
	Site × species	2, 31	2.25	0.122
	Site × litter	2, 31	0.73	0.489
	Species × litter	4, 31	27.43	**< 0.001**
	Site × species × litter	4, 31	2.01	0.117
Net N release	Site	1, 4	0.80	0.422
	Species	2, 31	3.99	0.029
	Litter	2, 31	2.39	0.108
	Site × species	2, 31	1.54	0.230
	Site × litter	2, 31	3.04	0.063
	Species × litter	4, 31	39.51	**< 0.001**
	Site × species × litter	4, 31	1.56	0.210
N uptake	Site	1, 4	0.43	0.547
	Species	2, 31	2.03	0.148
	Litter	2, 31	17.78	**< 0.001**
	Site × species	2, 31	0.18	0.838
	Site × litter	2, 31	2.19	0.129
	Species × litter	4, 31	3.23	**0.025**
	Site × species × litter	4, 31	1.86	0.142

Notes: Boldface type denotes a significant effect ($P < 0.05$).

Table A1.9. Pairwise comparisons of litter × species combinations for gross N release after 2.5 years of litter decomposition in mesh litterbags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Litter type 1	Species 1	Litter type 2	Species 2	P
foliage	bigleaf maple	roots	bigleaf maple	**0.001**
foliage	bigleaf maple	twigs	bigleaf maple	0.685
foliage	bigleaf maple	foliage	Sitka spruce	**< 0.001**
foliage	bigleaf maple	roots	Sitka spruce	0.699
foliage	bigleaf maple	twigs	Sitka spruce	0.104
foliage	bigleaf maple	foliage	Douglas-fir	**0.078**
foliage	bigleaf maple	roots	Douglas-fir	0.670
foliage	bigleaf maple	twigs	Douglas-fir	**0.003**
roots	bigleaf maple	twigs	bigleaf maple	0.250
roots	bigleaf maple	foliage	Sitka spruce	0.188
roots	bigleaf maple	roots	Sitka spruce	**0.017**
roots	bigleaf maple	twigs	Sitka spruce	**< 0.001**
roots	bigleaf maple	foliage	Douglas-fir	0.796
roots	bigleaf maple	roots	Douglas-fir	**0.020**
roots	bigleaf maple	twigs	Douglas-fir	1.000
twigs	bigleaf maple	foliage	Sitka spruce	**0.001**
twigs	bigleaf maple	roots	Sitka spruce	1.000
twigs	bigleaf maple	twigs	Sitka spruce	**0.001**
twigs	bigleaf maple	foliage	Douglas-fir	0.939
twigs	bigleaf maple	roots	Douglas-fir	1.000
twigs	bigleaf maple	twigs	Douglas-fir	0.179
foliage	Sitka spruce	roots	Sitka spruce	**< 0.001**
foliage	Sitka spruce	twigs	Sitka spruce	**< 0.001**
foliage	Sitka spruce	foliage	Douglas-fir	**0.011**
foliage	Sitka spruce	roots	Douglas-fir	**< 0.001**
foliage	Sitka spruce	twigs	Douglas-fir	0.458
roots	Sitka spruce	twigs	Sitka spruce	**0.003**
roots	Sitka spruce	foliage	Douglas-fir	0.707
roots	Sitka spruce	roots	Douglas-fir	1.000
roots	Sitka spruce	twigs	Douglas-fir	**0.046**
twigs	Sitka spruce	foliage	Douglas-fir	**< 0.001**
twigs	Sitka spruce	roots	Douglas-fir	**< 0.001**
twigs	Sitka spruce	twigs	Douglas-fir	**< 0.001**
foliage	Douglas-fir	roots	Douglas-fir	0.769
foliage	Douglas-fir	twigs	Douglas-fir	0.854
roots	Douglas-fir	twigs	Douglas-fir	0.142

Notes: Boldface type denotes a significant ($P < 0.05$) difference.

Table A1.10. Pairwise comparisons of litter × species combinations for net N release after 2.5 years of litter decomposition in mesh litterbags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Litter 1	Species 1	Litter 2	Species 2	P
foliage	bigleaf maple	roots	bigleaf maple	**< 0.001**
foliage	bigleaf maple	twigs	bigleaf maple	**< 0.001**
foliage	bigleaf maple	foliage	Sitka spruce	**< 0.001**
foliage	bigleaf maple	roots	Sitka spruce	**0.003**
foliage	bigleaf maple	twigs	Sitka spruce	0.443
foliage	bigleaf maple	foliage	Douglas-fir	**0.005**
foliage	bigleaf maple	roots	Douglas-fir	**0.004**
foliage	bigleaf maple	twigs	Douglas-fir	**< 0.001**
roots	bigleaf maple	twigs	bigleaf maple	0.996
roots	bigleaf maple	foliage	Sitka spruce	0.910
roots	bigleaf maple	roots	Sitka spruce	0.264
roots	bigleaf maple	twigs	Sitka spruce	**< 0.001**
roots	bigleaf maple	foliage	Douglas-fir	0.698
roots	bigleaf maple	roots	Douglas-fir	0.189
roots	bigleaf maple	twigs	Douglas-fir	0.681
twigs	bigleaf maple	foliage	Sitka spruce	0.448
twigs	bigleaf maple	roots	Sitka spruce	0.341
twigs	bigleaf maple	twigs	Sitka spruce	**< 0.001**
twigs	bigleaf maple	foliage	Douglas-fir	0.873
twigs	bigleaf maple	roots	Douglas-fir	0.232
twigs	bigleaf maple	twigs	Douglas-fir	**0.015**
foliage	Sitka spruce	roots	Sitka spruce	**0.024**
foliage	Sitka spruce	twigs	Sitka spruce	**< 0.001**
foliage	Sitka spruce	foliage	Douglas-fir	0.164
foliage	Sitka spruce	roots	Douglas-fir	**0.022**
foliage	Sitka spruce	twigs	Douglas-fir	1.000
roots	Sitka spruce	twigs	Sitka spruce	**0.005**
roots	Sitka spruce	foliage	Douglas-fir	1.000
roots	Sitka spruce	roots	Douglas-fir	1.000
roots	Sitka spruce	twigs	Douglas-fir	**< 0.001**
twigs	Sitka spruce	foliage	Douglas-fir	**0.023**
twigs	Sitka spruce	roots	Douglas-fir	**0.014**
twigs	Sitka spruce	twigs	Douglas-fir	**< 0.001**
foliage	Douglas-fir	roots	Douglas-fir	1.000
foliage	Douglas-fir	twigs	Douglas-fir	**0.020**
roots	Douglas-fir	twigs	Douglas-fir	**< 0.001**

Notes: Boldface type denotes a significant ($P < 0.05$) difference.

Table A1.11. Pairwise comparisons of litter × species combinations for N uptake after 2.5 years of litter decomposition in mesh litterbags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Litter 1	Species 1	Litter 2	Species 2	P
foliage	bigleaf maple	roots	bigleaf maple	0.942
foliage	bigleaf maple	twigs	bigleaf maple	**0.026**
foliage	bigleaf maple	foliage	Sitka spruce	1.000
foliage	bigleaf maple	roots	Sitka spruce	**0.033**
foliage	bigleaf maple	twigs	Sitka spruce	**< 0.001**
foliage	bigleaf maple	foliage	Douglas-fir	0.784
foliage	bigleaf maple	roots	Douglas-fir	0.063
foliage	bigleaf maple	twigs	Douglas-fir	0.520
roots	bigleaf maple	twigs	bigleaf maple	0.105
roots	bigleaf maple	foliage	Sitka spruce	0.670
roots	bigleaf maple	roots	Sitka spruce	0.439
roots	bigleaf maple	twigs	Sitka spruce	**0.004**
roots	bigleaf maple	foliage	Douglas-fir	1.000
roots	bigleaf maple	roots	Douglas-fir	0.613
roots	bigleaf maple	twigs	Douglas-fir	0.963
twigs	bigleaf maple	foliage	Sitka spruce	**0.017**
twigs	bigleaf maple	roots	Sitka spruce	0.997
twigs	bigleaf maple	twigs	Sitka spruce	0.674
twigs	bigleaf maple	foliage	Douglas-fir	0.348
twigs	bigleaf maple	roots	Douglas-fir	0.985
twigs	bigleaf maple	twigs	Douglas-fir	0.992
foliage	Sitka spruce	roots	Sitka spruce	**0.033**
foliage	Sitka spruce	twigs	Sitka spruce	**< 0.001**
foliage	Sitka spruce	foliage	Douglas-fir	0.517
foliage	Sitka spruce	roots	Douglas-fir	**0.020**
foliage	Sitka spruce	twigs	Douglas-fir	0.366
roots	Sitka spruce	twigs	Sitka spruce	**0.019**
roots	Sitka spruce	foliage	Douglas-fir	0.508
roots	Sitka spruce	roots	Douglas-fir	1.000
roots	Sitka spruce	twigs	Douglas-fir	1.000
twigs	Sitka spruce	foliage	Douglas-fir	**0.005**
twigs	Sitka spruce	roots	Douglas-fir	0.110
twigs	Sitka spruce	twigs	Douglas-fir	0.264
foliage	Douglas-fir	roots	Douglas-fir	0.817
foliage	Douglas-fir	twigs	Douglas-fir	0.975
roots	Douglas-fir	twigs	Douglas-fir	1.000

Notes: Boldface type denotes a significant ($P < 0.05$) difference.

Table A1.12. Results from repeated measures ANOVA for N release and uptake per time interval for litter decomposed in mesh litterbags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Dependent variable	Fixed effect	DF	F value	P
Total N release	Site	1, 4	0.06	0.818
	Species	2, 103	0.61	0.545
	Site × Species	2, 103	0.15	0.857
	Time	2, 103	0.90	0.412
	Site × Time	2, 103	2.13	0.124
	Species × Time	4, 103	0.85	0.499
	Site × Species × Time	4, 103	1.47	0.217
	Litter	2, 103	4.38	**0.015**
	Site × Litter	2, 103	0.10	0.902
	Species × Litter	4, 103	3.65	**0.008**
	Site × Species × Litter	4, 103	0.26	0.906
	Time × Litter	4, 103	1.04	0.392
	Site × Time × Litter	4, 103	0.21	0.930
	Species × Time × Litter	8, 103	1.69	0.111
	Site × Species × Time × Litter	8, 103	1.81	0.084
Net N release	Site	1, 4	0.56	0.494
	Species	2, 103	0.91	0.405
	Site × Species	2, 103	0.21	0.809
	Time	2, 103	10.90	**< 0.001**
	Site × Time	2, 103	0.24	0.784
	Species × Time	4, 103	0.70	0.593
	Site × Species × Time	4, 103	1.07	0.373
	Litter	2, 103	4.09	**0.020**
	Site × Litter	2, 103	0.38	0.683
	Species × Litter	4, 103	12.84	**< 0.001**
	Site × Species × Litter	4, 103	0.14	0.968
	Time × Litter	4, 103	5.64	**< 0.001**
	Site × Time × Litter	4, 103	1.27	0.288
	Species × Time × Litter	8, 103	4.27	**< 0.001**
	Site × Species × Time × Litter	8, 103	0.78	0.622

Notes: Boldface type denotes a significant effect ($P < 0.05$).

Table A12. Continued.

Dependent variable	Fixed effect	DF	F value	P
N uptake	Site	1, 4	0.21	0.670
	Species	2, 103	0.50	0.606
	Site × Species	2, 103	0.00	1.000
	Time	2, 103	5.44	0.006
	Site × Time	2, 103	1.68	0.191
	Species × Time	4, 103	0.84	0.501
	Site × Species × Time	4, 103	4.25	**0.003**
	Litter	2, 103	1.93	0.150
	Site × Litter	2, 103	0.15	0.857
	Species × Litter	4, 103	0.23	0.920
	Site × Species × Litter	4, 103	0.21	0.930
	Time × Litter	4, 103	2.71	**0.034**
	Site × Time × Litter	4, 103	0.22	0.925
	Species × Time × Litter	8, 103	0.99	0.449
	Site × Species × Time × Litter	8, 103	1.51	0.161

Table A1.13. N release and uptake per time interval for litter decomposed in mesh litterbags at Cascade Head Experimental Forest and H.J. Andrews Experimental Forest.

Litter type	Species	Time (yr)	Gross N release (% of initial N)	Net N release (% of initial N)	N uptake (% of initial N)	P*
Foliage	bigleaf maple	0-0.25	9.09 ± 7.86	11.80 ± 4.82	-2.71 ± 7.29	0.654
		0.25-1	10.29 ± 7.86	-1.47 ± 4.82	11.76 ± 7.29	**0.041**
		1-2.5	5.63 ± 8.71	-3.39 ± 5.33	7.29 ± 8.06	0.198
	Douglas-fir	0-0.25	18.24 ± 7.86	19.22 ± 4.82	-0.98 ± 7.29	0.353
		0.25-1	16.93 ± 7.86	7.61 ± 4.82	9.32 ± 7.29	**0.002**
		1-2.5	21.61 ± 7.86	14.56 ± 4.82	7.05 ± 7.29	**0.011**
	Sitka spruce	0-0.25	18.25 ± 7.86	22.26 ± 4.82	-4.01 ± 7.29	**0.008**
		0.25-1	9.37 ± 7.86	13.27 ± 4.82	-3.90 ± 7.29	0.793
		1-2.5	43.66 ± 7.86	24.76 ± 4.82	18.90 ± 7.29	0.226
Roots	bigleaf maple	0-0.25	25.45 ± 5.91	24.75 ± 4.10	0.70 ± 4.29	0.867
		0.25-1	14.77 ± 5.91	4.74 ± 4.10	10.03 ± 4.29	**0.033**
		1-2.5	17.88 ± 6.16	16.27 ± 4.20	1.33 ± 4.50	0.478
	Douglas-fir	0-0.25	8.25 ± 5.91	15.24 ± 4.10	-6.99 ± 4.29	**0.015**
		0.25-1	14.10 ± 5.91	3.98 ± 4.10	10.13 ± 4.29	**0.031**
		1-2.5	12.63 ± 5.91	9.95 ± 4.10	2.68 ± 4.29	0.600
	Sitka spruce	0-0.25	17.74 ± 5.91	20.06 ± 4.10	-2.32 ± 4.29	0.738
		0.25-1	7.07 ± 5.91	-0.57 ± 4.10	7.64 ± 4.29	0.305
		1-2.5	10.48 ± 5.91	10.87 ± 4.10	-0.39 ± 4.29	0.919

Notes: Values are means ± SE; $n = 6$.

* Results from a single-sample t-test on the difference between gross N release and net N release per time interval. Boldface type denotes a significant ($P < 0.05$) difference.

Table A1.13. Continued.

Litter type	Species	Time (yr)	Total N release (% of initial N)	Net N release (% of initial N)	N uptake (% of initial N)	P*
Twigs	bigleaf maple	0-0.25	8.06 ± 4.21	1.79 ± 2.50	6.27 ± 4.35	0.342
		0.25-1	12.85 ± 4.21	15.80 ± 2.50	-2.95 ± 4.35	0.731
		1-2.5	7.56 ± 4.42	12.12 ± 2.66	-3.31 ± 4.26	0.239
	Douglas-fir	0-0.25	19.95 ± 4.21	21.91 ± 2.50	-1.96 ± 4.35	0.382
		0.25-1	8.13 ± 4.21	4.52 ± 2.50	3.61 ± 4.35	0.192
		1-2.5	13.74 ± 4.21	10.14 ± 2.50	3.60 ± 4.35	0.223
	Sitka spruce	0-0.25	0.31 ± 4.21	2.72 ± 2.50	-2.42 ± 4.35	0.525
		0.25-1	7.66 ± 4.21	4.12 ± 2.50	3.54 ± 4.35	0.373
		1-2.5	-3.14 ± 4.21	3.68 ± 2.50	-6.82 ± 4.35	**0.086**

Table A1.14. Pearson correlation coefficients (r) for decomposition rate constants, gross and net N mineralization, and N uptake versus initial litter chemistry constituents.

Litter type	Variable	Initial lignin	Initial N	Initial C:N
Foliage	Integrated *k*	-0.428	0.427	-0.439
	k_e	-0.709**	0.897**	-0.901**
	Gross N mineralization	0.858**	-0.747**	0.782**
	Net N mineralization	0.786**	-0.807**	0.829**
	N uptake	-0.144	-0.214	0.181
Roots	Integrated *k*	-0.680**	0.610**	-0.509*
	k_e	-0.597**	0.603**	-0.529*
	Gross N mineralization	0.626**	-0.812**	0.776**
	Net N mineralization	0.429	-0.533*	0.503*
	N uptake	-0.323	0.483*	-0.479*
Twigs	Integrated *k*	-0.577*	0.525*	-0.565*
	k_e	-0.596**	0.738**	-0.747**
	Gross N mineralization	0.401	-0.840**	0.789**
	Net N mineralization	0.474*	-0.897**	0.853**
	N uptake	-0.200	0.527*	-0.484*

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

Table A1.15. Biomass estimates and N content estimates for used to calculate potential N release from disturbance.

Site and species	Age class	Age (yr)	Foliage biomass† (kg C·ha^{-1})	Foliage N (g N·kg^{-1} C)	Foliage N (kg N·ha^{-1})	Fine root biomass† (kg C·ha^{-1})	Fine root N (g N·kg^{-1} C)	Fine root N (kg N·ha^{-1})	Twig biomass* (kg C·ha^{-1})	Twig N (g N·kg^{-1} C)	Twig N (kg N·ha^{-1})
Coast	Initiation	>12-14	8830	27.61	243.84	1990	22.93	45.63	3302	16.97	56.04
Douglas-fir	Young	22-40	7000	27.61	193.30	2010	22.93	46.08	2618	16.97	44.42
	Mature	45-52	6720	27.61	185.57	1510	22.93	34.62	2513	16.97	42.65
	Old	170-190	5230	27.61	144.43	1740	22.93	39.89	1956	16.97	33.19
Coast	Initiation	>12-14	8830	28.34	250.23	1990	22.36	44.50	3302	12.65	41.77
Sitka spruce	Young	22-40	7000	28.34	198.37	2010	22.36	44.95	2618	12.65	33.12
	Mature	45-52	6720	28.34	190.43	1510	22.36	33.77	2513	12.65	31.79
	Old	170-190	5230	28.34	148.21	1740	22.36	38.91	1956	12.65	24.74
West Cascades	Initiation	>12-14	3860	23.01	88.83	3180	24.91	79.20	46320	17.46	808.75
bigleaf maple	Young	22-40	7200	23.01	165.70	2390	24.91	59.53	86400	17.46	1508.54
	Mature	45-52	11050	23.01	254.30	2990	24.91	74.47	132600	17.46	2315.20
	Old	170-190	7230	23.01	166.39	2500	24.91	62.27	86760	17.46	1514.83
West Cascades	Initiation	>12-14	3860	27.61	106.59	3180	22.93	72.91	1444	16.97	24.50
Douglas-fir	Young	22-40	7200	27.61	198.83	2390	22.93	54.80	2693	16.97	45.69
	Mature	45-52	11050	27.61	305.14	2990	22.93	68.55	4132	16.97	70.13
	Old	170-190	7230	27.61	199.66	2500	22.93	57.32	2704	16.97	45.88

† From Campbell et. al (2004).

* van Huysen, unpublished data.

Notes: Foliage N and fine root N were calculated by applying N content data generated from my study to the biomass estimates from Campbell et. al (2004). Twig N was calculated by applying N content data generated from my study to biomass estimates from van Huysen, unpublished data. Biomass estimates were not weighted by species.

APPENDIX 2:
CHAPTER 3 SUPLLEMENTAL MATERIAL

Table A2.1. Litter C, N, and P concentrations after 2 years of decomposition at three sites in the Oregon Coast Range.

Site	Litter type	Treatment†	C ($mg \cdot g^{-1}$)	N ($mg \cdot g^{-1}$)	P ($mg \cdot g^{-1}$)
5	Foliage	control	547.58 ± 26.85	23.03 ± 1.81	1.24 ± 0.15
		plant P	567.94 ± 26.85	25.49 ± 1.81	1.56 ± 0.15
		soil P	521.61 ± 26.85	22.96 ± 1.81	1.45 ± 0.15
		plant P × soil P	635.25 ± 26.85	28.90 ± 1.81	1.40 ± 0.15
	Roots	control	506.44 ± 26.85	15.72 ± 1.81	1.12 ± 0.15
		plant P	499.28 ± 26.85	18.36 ± 1.81	1.56 ± 0.15
		soil P	497.29 ± 26.85	16.35 ± 1.81	1.25 ± 0.15
		plant P × soil P	504.73 ± 26.85	18.71 ± 1.81	1.40 ± 0.15
	Twigs	control	560.07 ± 26.85	9.76 ± 1.81	0.57 ± 0.15
		plant P	561.13 ± 26.85	10.80 ± 1.81	0.62 ± 0.15
		soil P	554.23 ± 26.85	9.16 ± 1.81	0.51 ± 0.15
		plant P × soil P	572.78 ± 26.85	12.07 ± 1.81	0.71 ± 0.15
39	Foliage	control	514.91 ± 32.82	22.87 ± 2.19	1.35 ± 0.18
		plant P	519.37 ± 26.85	24.39 ± 1.81	1.45 ± 0.15
		soil P	512.80 ± 26.85	24.16 ± 1.81	1.86 ± 0.15
		plant P × soil P	515.28 ± 26.85	25.52 ± 1.81	1.82 ± 0.15
	Roots	control	492.90 ± 26.85	16.96 ± 1.81	1.15 ± 0.15
		plant P	509.25 ± 26.85	19.89 ± 1.81	1.41 ± 0.15
		soil P	507.18 ± 26.85	18.83 ± 1.81	1.40 ± 0.15
		plant P × soil P	488.48 ± 32.85	19.40 ± 2.19	1.51 ± 0.18
	Twigs	control	539.71 ± 26.85	9.77 ± 1.81	0.56 ± 0.15
		plant P	577.01 ± 26.85	16.16 ± 1.81	0.91 ± 0.15
		soil P	571.25 ± 26.85	10.72 ± 1.81	0.65 ± 0.15
		plant P × soil P	572.01 ± 32.85	12.77 ± 2.19	0.76 ± 0.15
58	Foliage	control	522.45 ± 26.85	22.24 ± 1.81	1.43 ± 0.15
		plant P	502.46 ± 26.85	22.80 ± 1.81	1.79 ± 0.18
		soil P	518.01 ± 26.85	20.11 ± 1.81	1.44 ± 0.15
		plant P × soil P	466.56 ± 26.85	22.85 ± 1.81	1.93 ± 0.15
	Roots	control	504.12 ± 26.85	17.88 ± 1.81	1.25 ± 0.15
		plant P	508.93 ± 26.85	18.21 ± 1.81	1.41 ± 0.18
		soil P	452.84 ± 26.85	16.74 ± 1.81	1.32 ± 0.18
		plant P × soil P	512.37 ± 26.85	19.65 ± 1.81	1.33 ± 0.15
	Twigs	control	547.54 ± 32.82	12.68 ± 2.19	0.78 ± 0.18
		plant P	532.03 ± 26.85	8.67 ± 1.81	0.36 ± 0.15
		soil P	555.59 ± 26.85	9.08 ± 1.81	0.56 ± 0.15
		plant P × soil P	543.35 ± 26.85	12.81 ± 1.81	0.80 ± 0.15

Notes: Values are means ± SE; $n = 3$.

† Control: no P fertilization, plant P: P-fertilized litter only, soil P: soil P-fertilized only, plant P × soil P: P-fertilized litter and soil P-fertilized.

Table A2.2. C, N, and P mineralization after 2 years of litter decomposition at three sites in the Oregon Coast Range.

Site	Litter type	Treatment†	C release (% of initial)	N release (% of initial)	P release (% of initial)
5	Foliage	control	68.09 ± 6.65	54.95 ± 9.26	74.02 ± 5.28
		plant P	47.44 ± 6.65	28.94 ± 9.26	91.29 ± 5.28
		soil P	50.26 ± 6.65	27.43 ± 9.26	53.12 ± 5.28
		plant P × soil P	46.57 ± 6.65	27.00 ± 9.26	92.82 ± 5.28
	Roots	control	46.63 ± 6.65	14.99 ± 9.26	63.09 ± 5.28
		plant P	41.27 ± 6.65	10.70 ± 9.26	74.86 ± 5.28
		soil P	44.04 ± 6.65	5.93 ± 9.26	56.56 ± 5.28
		plant P × soil P	40.72 ± 6.65	9.00 ± 9.26	77.15 ± 5.28
	Twigs	control	30.84 ± 6.65	27.75 ± 9.26	76.60 ± 5.28
		plant P	22.67 ± 6.65	45.65 ± 9.26	90.07 ± 5.28
		soil P	22.67 ± 6.65	22.42 ± 9.26	76.06 ± 5.28
		plant P × soil P	68.31 ± 6.65	79.01 ± 9.26	96.09 ± 5.28
39	Foliage	control	69.00 ± 8.07	52.35 ± 11.31	71.08 ± 6.41
		plant P	55.30 ± 6.65	36.59 ± 9.26	92.42 ± 5.28
		soil P	47.58 ± 6.65	18.87 ± 9.26	34.98 ± 5.28
		plant P × soil P	52.92 ± 6.65	29.61 ± 9.26	89.69 ± 5.28
	Roots	control	50.64 ± 6.65	12.80 ± 9.26	64.36 ± 5.28
		plant P	50.02 ± 6.65	18.91 ± 9.26	80.77 ± 5.28
		soil P	46.21 ± 6.65	0.45 ± 9.26	54.97 ± 5.28
		plant P × soil P	46.21 ± 8.10	12.25 ± 11.32	77.00 ± 6.41
	Twigs	control	28.10 ± 6.65	21.45 ± 9.26	75.24 ± 5.28
		plant P	40.36 ± 6.65	36.98 ± 9.26	88.53 ± 5.28
		soil P	45.20 ± 6.65	38.58 ± 9.26	79.46 ± 5.28
		plant P × soil P	31.57 ± 8.10	41.41 ± 11.32	87.92 ± 6.41
58	Foliage	control	55.60 ± 6.65	36.71 ± 9.26	57.19 ± 5.28
		plant P	54.92 ± 6.65	37.62 ± 9.26	87.43 ± 6.41
		soil P	51.05 ± 6.65	35.75 ± 9.26	54.02 ± 5.28
		plant P × soil P	45.33 ± 6.65	19.56 ± 9.26	85.34 ± 5.28
	Roots	control	40.70 ± 6.65	-6.72 ± 9.26	54.93 ± 5.28
		plant P	36.50 ± 6.65	5.97 ± 9.26	76.14 ± 6.41
		soil P	47.10 ± 6.65	-0.86 ± 9.26	54.88 ± 6.41
		plant P × soil P	42.08 ± 6.65	8.15 ± 9.26	79.24 ± 5.28
	Twigs	control	27.80 ± 8.07	-2.95 ± 11.31	64.49 ± 6.41
		plant P	18.29 ± 6.65	51.13 ± 9.26	93.33 ± 5.28
		soil P	22.31 ± 6.65	22.13 ± 9.26	73.07 ± 5.28
		plant P × soil P	34.36 ± 6.65	45.50 ± 9.26	88.65 ± 5.28

Notes: Values are means ± SE; $n = 3$.

† Control: no P fertilization, plant P: P-fertilized litter only, soil P: soil P-fertilized only, plant P × soil P: P-fertilized litter and soil P-fertilized.

Table A2.3. Litter element ratios after 2 years of decomposition at three sites in the Oregon Coast Range.

Site	Litter type	Treatment†	C:N (mass:mass)	C:P (mass:mass)	N:P (mass:mass)
5	Foliage	control	23.80 (- 2.45, + 3.09)	446.13 (- 125.51, + 286.99)	18.74 (- 1.89, + 2.37)
5		plant P	22.36 (- 2.31, + 2.91)	363.92 (- 102.38, + 234.1)	16.28 (- 1.64, + 2.06)
5		soil P	22.74 (- 2.34, + 2.95)	364.45 (- 102.53, + 234.44)	16.04 (- 1.62, + 2.03)
5		plant P × soil P	22.31 (- 2.30, + 2.9)	442.37 (- 124.45, + 284.57)	19.83 (- 2.00, + 2.5)
5	Roots	control	32.38 (- 3.34, + 4.21)	454.60 (- 127.89, + 292.43)	14.04 (- 1.42, + 1.77)
5		plant P	27.22 (- 2.81, + 3.54)	327.11 (- 92.03, + 210.43)	12.01 (- 1.21, + 1.52)
5		soil P	30.41 (- 3.14, + 3.95)	399.58 (- 112.41, + 257.04)	13.13 (- 1.32, + 1.66)
5		plant P × soil P	27.01 (- 2.79, + 3.51)	361.52 (- 101.71, + 232.56)	13.38 (- 1.35, + 1.69)
5	Twigs	control	58.17 (- 6.00, + 7.56)	1013.39 (- 285.10, + 651.9)	17.42 (- 1.76, + 2.2)
5		plant P	55.19 (- 5.69, + 7.17)	979.95 (- 275.69, + 630.39)	17.76 (- 1.79, + 2.24)
5		soil P	64.13 (- 6.61, + 8.33)	1207.16 (- 339.61, + 776.55)	18.83 (- 1.90, + 2.38)
5		plant P × soil P	48.30 (- 4.98, + 6.28)	826.97 (- 232.65, + 531.98)	17.12 (- 1.73, + 2.16)
39	Foliage	control	22.29 (- 2.75, + 3.64)	376.82 (- 119.80, + 328.98)	16.70 (- 1.98, + 2.59)
39		plant P	21.24 (- 2.19, + 2.76)	357.12 (- 100.47, + 229.73)	16.81 (- 1.69, + 2.12)
39		soil P	21.28 (- 2.20, + 2.77)	282.25 (- 79.41, + 181.57)	13.26 (- 1.34, + 1.67)
39		plant P × soil P	20.18 (- 2.08, + 2.62)	287.45 (- 80.87, + 184.91)	14.26 (- 1.44, + 1.8)
39	Roots	control	29.01 (- 2.99, + 3.77)	429.25 (- 120.76, + 276.13)	14.80 (- 1.49, + 1.87)
39		plant P	25.63 (- 2.64, + 3.33)	363.29 (- 102.21, + 233.7)	14.17 (- 1.43, + 1.79)
39		soil P	27.08 (- 2.79, + 3.52)	363.13 (- 102.16, + 233.6)	13.41 (- 1.35, + 1.69)
39		plant P × soil P	25.04 (- 3.08, + 4.09)	323.10 (- 102.74, + 282.24)	12.51 (- 1.49, + 1.95)

Notes: Values are back-transformed means (- lower SD, + upper SD); $n = 3$.

† Control: no P fertilization, plant P: P-fertilized litter only, soil P: soil P-fertilized only, plant P × soil P: P-fertilized litter and soil P-fertilized.

Table A2.3. Continued.

Site	Litter type	Treatment†	C:N (mass:mass)	C:P (mass:mass)	N:P (mass:mass)
39	Twigs	control	59.80 (- 6.17, + 7.77)	1076.97 (- 302.99, + 692.8)	18.01 (- 1.82, + 2.27)
		plant P	35.86 (- 3.70, + 4.66)	639.93 (- 180.03, + 411.66)	17.86 (- 1.80, + 2.26)
		soil P	54.14 (- 5.58, + 7.03)	906.10 (- 254.92, + 582.88)	16.73 (- 1.69, + 2.11)
		plant P × soil P	43.98 (- 5.42, + 7.19)	704.01 (- 223.87, + 614.98)	15.52 (- 1.85, + 2.42)
58	Foliage	control	23.45 (- 2.42, + 3.05)	374.72 (- 105.42, + 241.05)	15.99 (- 1.61, + 2.02)
		plant P	22.04 (- 2.27, + 2.86)	260.59 (- 82.84, + 227.47)	12.60 (- 1.49, + 1.96)
		soil P	26.19 (- 2.70, + 3.4)	363.12 (- 102.16, + 233.59)	13.86 (- 1.40, + 1.75)
		plant P × soil P	20.44 (- 2.11, + 2.66)	250.19 (- 70.39, + 160.94)	12.25 (- 1.24, + 1.55)
	Roots	control	28.27 (- 2.92, + 3.67)	405.64 (- 114.12, + 260.94)	14.35 (- 1.45, + 1.81)
		plant P	27.98 (- 2.89, + 3.64)	373.29 (- 118.68, + 325.89)	13.15 (- 1.56, + 2.04)
		soil P	26.84 (- 2.77, + 3.49)	390.80 (- 124.24, + 341.14)	13.12 (- 1.55, + 2.03)
		plant P × soil P	26.09 (- 2.69, + 3.39)	384.91 (- 108.29, + 247.6)	14.75 (- 1.49, + 1.86)
	Twigs	control	43.64 (- 5.37, + 7.13)	80.96 (- 22.78, + 52.08)	15.91 (- 1.88, + 2.47)
		plant P	64.46 (- 6.65, + 8.37)	1494.37 (- 420.42, + 961.31)	23.19 (- 2.34, + 2.93)
		soil P	62.09 (- 6.40, + 8.07)	1010.43 (- 284.27, + 649.99)	16.27 (- 1.64, + 2.05)
		plant P × soil P	45.83 (- 4.73, + 5.95)	690.45 (- 194.25, + 444.16)	15.06 (- 1.52, + 1.9)

Table A2.4. Pearson correlation coefficients (r) for decomposition rate constant, N release, and P release versus initial litter chemistry constituents and N and P release.

Variable	k_e	Initial N concentration	Initial P concentration	Initial C:N	Initial C:P	Initial N:P	N release	P release
k_e	n.a.	0.80**	0.47**	-0.71**	-0.20	0.18	-0.29	-0.05
N release	-0.29	-0.44**	-0.21	0.40**	0.23	-0.01	n.a.	0.52**
P release	-0.05	-0.25	-0.69**	0.24	0.78**	0.79**	0.52**	n.a.

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