AN ABSTRACT OF THE THESIS OF

Joselin J. Matkins for the degree of Master of Science in Forest Science presented on March19, 2009.
Title: Decomposition and Nitrogen Dynamics of Red Alder and Douglas-fir Leaf Litter in Oregon Coast Range Riparian Forests

Abstract approved:

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Steven S. Perakis David E. Hibbs

I examined factors regulating decomposition rates of red alder (*Alnus rubra))* and Douglas-fir *(Pseudotsuga menziesii)* leaf litter in Coast Range riparian areas in western Oregon. Overall, this study was designed to examine the influence that leaf litter quality characteristics and decomposition site treatment have on decomposition rates, to provide a better understanding of how vegetation management can impact nutritional subsidies and nutrient cycles within these riparian systems. I employed the litterbag method to compare decomposition rates of litter with different initial chemistry in sites of different N availability.

Specifically, this study investigates the role of litter source, riparian decomposition site, and how differences in N (both endogenous and exogenous) may influence the decomposition dynamics of red alder and Douglas-fir leaf litter. I addressed the following research questions: 1) How do the decomposition rates of red

alder and Douglas-fir differ? 2) Do differences in chemical measures of initial litter quality (eg. N, Ca, lignin, cellulose, C:N) correlate with different rates of decomposition in Douglas-fir (8 different sources of Douglas-fir litter)? 3) Does dominance of a site by either red alder or Douglas-fir overstory) influence decomposition rates? 4) Does N fertilization increase the rate of litter decomposition under Douglas-fir overstories?

Results suggest that red alder litter decomposes more rapidly than Douglas-fir litter under either canopy, but the difference in decomposition rates is greater under a red alder overstory than under a Douglas-fir overstory. N mineralization began immediately following placement of the red alder litter bags and more N was mineralized in red alder litter decomposing under red alder overstories than under Douglas-fir overstories. Compared to red alder, Douglas-fir litter decomposition did not vary by overstory treatment. Generally, Douglas-fir litter went through an immobilization period, with only high N litter mineralizing N under unfertilized Douglas-fir overstories. Both low- and high-N Douglas-fir litter immobilized more N under red alder overstories, and under fertilized Douglas-fir conditions. In fertilized plots under Douglas-fir overstories, high-N litter was still immobilizing N after two years. In contrast, low-N Douglas-fir litter immobilized N throughout the 2 year period under all treatments. This study indicates strong species-specific effect of overstory composition on riparian ecosystem processes. These effects can influence energy and nutrient budgets of riparian food webs, and suggest a need for broader

consideration of potential impacts resulting from conversion of red alder to Douglas-fir dominated riparian area.

Surprisingly, rates of Douglas-fir litter decomposition were negatively related to initial litter nitrogen concentrations across the range 0.7 – 1.4% N, contrary to patterns observed across species in other ecosystems. N fertilization exerted a minor influence on decomposition rates of Douglas-fir, with decomposition rates slower in fertilized Douglas-fir plots. These results highlight the complicated relationship between decomposition of high lignin litter and N availability and suggest that under such conditions decomposition can be dramatically reduced.

Decomposition and Nitrogen Dynamics of Red Alder and Douglas-fir Leaf Litter in Oregon Coast Range Riparian Forests

by
Joselin Matkins

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented (March 19, 2009)
Commencement (June 2009)

Master of Science thesis of Joselin Matkins presented on (March 19, 2009).

APPROVED:

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Major Professor, representing (Forest Ecosystems and Society)

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Head of the Department of Forest Science

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I understand that my thesis will become part of the permanent collection……..

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Joselin J. Matkins

ACKNOWLEDGEMENTS

Completing this thesis research was as an adventure of a lifetime, at times seemingly never ending. First and foremost, I want to thank Steve Perakis and David Hibbs for taking me on as a student, and more importantly, maintaining faith in me as I worked my way through several difficult years. I also want to thank committee members Mark Harmon and Manuela Huso for their important contributions to this work. From the Perakis Lab, I want to thank Chris Catricala for all her help over the years. To all the graduate students, lab and field partners, and friends I met along the way (Jake Adams, Emily Beamguard, Alison Cross, Stephanie Hart, Emily Scott, Amy Eckert, Carlos Sierra, Emily Sinkhon, Aaron Thiel, Tiffany Van Huysen, and Travis Wolley). You guys are dedicated, and I wish you all the best!

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CHAPTER ONE - INTRODUCTION

Current management regulations in Oregon promote the conversion of red alder (*Alnus rubra*) dominated riparian forests to conifer-dominated forests, in part to increase long-term supplies of structural large wood debris (LWD) to streams. However, little is known about how changes to the energetic and nutrient cycles associated with red alder could impact aquatic and riparian food chains. Encouraging the growth of conifer species over red alder may alter long standing nutritional subsidies and nutrient cycles within these systems. Understanding how and when carbon (as energy) and nutrients are taken in and made available for primary and secondary productivity in foodwebs is critical to understanding the structure and function of riparian zones in the Oregon Coast Range.

Through the process of leaf litter decomposition, energy and nutrients contained in senesced plant material are released, fueling microbial growth and making nutrients available for plants (Waring and Schlesinger 1985). At a global scale, decomposition of leaf litter is governed by complex interactions among chemical, physical, and biological processes (Witkamp 1971, Swift et al. 1979), and is ultimately constrained by climatic factors that regulate the activity of decomposer microorganisms, particularly temperature and moisture regimes (Bunnell and Tait 1974, Swift et al. 1979). Regionally, aspects related to litter quality (Meentemeyer 1978) and site of decomposition are important determinants of decomposition rates (Aber et al. 1991).

Factors of litter quality play a key role in determining the rate and temporal pattern of decomposition of a particular species (Aber and Melillo 1982, Harmon et al. 1990). The initial litter quality is defined as the relative composition of nutrients and carbon compounds contained in freshly senesced litter. The commonly accepted paradigm is that litter containing more easily digestible carbon and readily available nutrients decompose more rapidly than litter containing more resistant carbon compounds and fewer available nutrients (Hobbie and Vitousek 2000). The majority of decomposition studies have reported positive correlations between decomposition rates and initial nutrient concentrations and negative correlations with complex carbon compounds such as lignin (Melin 1930, Fogel and Cromack 1977, Cromack 1973, Mellillo et al. 1982, Berg and McClaugherty 1989, Aber et al. 1990, Harmon et al. 1990, Taylor et al. 1991, Hobbie 2000, Prescott et al. 2000).

The degree to which any one component of litter promotes or inhibits decomposition depends on the ease with which the nutrients in the litter can be made available, which relates to the biochemical complexity of the carbon compounds (Berg and McClaugherty 2003, Hobbie and Vitousek 2000). Sugars, amino acids and other easily decomposable components of leaf litter that decompose relatively rapidly are categorized as labile metabolic compounds. Compared to more recalcitrant compounds, this component of the litter is rich in available nutrients and simple carbon compounds. Moderately labile structural compounds (cellulose and hemicellulose) decompose more slowly and structural material (lignin) tends to be most resistant to decomposition. While a wide variety of decomposer organisms can

degrade cellulytic compounds, only white rot fungi can degrade lignin (Kirk and Farrell 1987). In temperate forests, the lignin:N ratio has served as an effective predictor of leaf litter decomposition rates across many coniferous and broadleaf species (Melillo et al. 1982 and 1984, Aber and Mellilo 1991, Harmon et al. 1990, Valachovic 1998). These studies all report faster decomposition of litter with the lower lignin:N ratios than litter with higher lignin:N ratios.

Although these broad generalities have been developed by examining patterns of litter decomposition across species, there is little information on how variations in quality within a single species might influence decomposition rates. Different tree species can vary widely in leaf structural attributes that may influence decomposition independently of overall leaf chemistry. Foliage of a single tree species in different stands can vary widely in chemical makeup, providing an opportunity to control pecies differences in leaf structure while evaluating chemical controls on decomposition. Several studies have shown that lignin:N is negatively correlated to decomposition rate across species (Mellillo et al. 1982, Berg and McClaugherty 1989, Aber et al. 1990, Harmon et al. 1990, Taylor et al. 1991, Hobbie 2000, Prescott et al. 2000), but only a few studies have evaluated this relationship within a single species and results have been mixed (Prescott 1995, Berg et al.1982). While neither Prescott (1995) nor Berg et al.(1982) found a difference between decomposition rates of litter of the same species despite initial differences in N concentrations, Berg et al. (1982) found that lignin decomposition of Scots pine (*Pinus vestris)* was reduced in litter with higher initial N.

Complicating our understanding of the traditional lignin-N paradigm is mounting evidence that suggests the relationship between N availability and decomposition rates does not align with traditional expectations for high lignin litter (Knorr et al. 2006, Fog 1988). Several studies have shown that increasing N in high lignin environments (particularly in boreal and temperate forests) can reduce decomposition by suppressing the enzymatic system that breaks down lignin (Knorr et al. 2006, Herman et al. 1977, Berg et al. 1982, Berg et al. 1987, Fog 1988, Prescott et al. 2004, Fog 1988, Sinsabaugh 2000, Carreiro et al. 2000). Evaluating decomposition of litters from a single species that ranges widely in N content, but which varies relatively little in lignin, provides an opportunity to isolate the influence that internal tissue N content has on litter decomposition and thus improve our understanding of biogeochemical controls on decomposition overall.

In addition to litter quality factors, there are several other factors that can influence decomposition rates including environmental factors, UV light, and composition of the soil community. Key environmental factors include nutrient availability (Prescott 1995), forest community composition (Hunt et al. 1988), and soil temperature and moisture (Fogel and Cromack 1977). Comparisons of leaf breakdown in nutrient-poor versus more nutrient-rich systems have often demonstrated faster breakdown rates in a nutrient-rich system (particularly in regard to nitrogen) (Hunt et al. 1988). However, Prescott (1995) found that N amendments did not increase decomposition rates. Vesterdal (1999) found that the influence of site depended on the species tested and that high quality litter decomposed more rapidly in

its forest of origin. In addition, site characteristics that promote or inhibit microbial growth and respiration can play a key role in determining decomposition rate. Hunt et al. (1988) argued that the nature of microorganisms and soil fauna active in the decomposition process regulates decomposition. Schaefer and Schauermann (1990) demonstrated that nutrient status can influence the decomposer community composition, activity, and biomass. Given the diversity of soil ecosystems and decomposer fauna, it is plausible that any combination of these factors may ultimately regulate decomposition at a particular site.

The Role of Decomposition in Riparian Forests

Riparian areas surrounding headwater streams in the Oregon Coast Range are transitional systems whose structure and function at any given time is the result of complex interactions between abiotic and biotic factors. In Oregon Coast Range riparian forests, stands of Douglas-fir *(Pseudotsuga menziesii)* and other conifers contribute to riparian ecosystem function through the input of large woody debris (LWD) that is resistant to decomposition and year round shade, both of which are critical for fish habitat. Riparian forests dominated by nitrogen-fixing red alder provide only seasonal shade, and because red alder wood decomposes rapidly, provide only short lived structural wood to streams (Anderson et al. 1978, Gregory et al.1991). However, through leaf litter inputs, red alder contributes large amounts of energy and nutrients that are thought to be more readily available than those locked in Douglas-fir needles. Red alder has litter N concentrations two to three times higher than Douglas-

fir (Valachovic 1998, Scott 2004), which increases the availability of N in the riparian soils.

In coordination with Cooperative Forest Ecosystem Research Program (CFER), which has examined how vegetation composition and the physical characteristics of riparian zones influence the delivery of leaf litter to riparian soils and streams in both alder- and conifer-dominated riparian systems, this study will expand our understanding of nutrient cycling of red alder and Douglas-fir – two key species in Oregon Coast Range riparian areas. Specifically, this study investigates the role of litter source, riparian decomposition site, and how differences in N (both endogenous and exogenous) may influence the decomposition dynamics of red alder and Douglas-fir leaf litter.

Chapter 2 of this thesis evaluates the rate and temporal pattern (the pattern of biomass loss over time, e.g., consistent proportional decomposition versus periods of rapid mass loss then periods of reduced mass loss) of decomposition of red alder and Douglas-fir foliar litter under red alder and Douglas-fir overstories in Coast Range riparian areas. I examined differences in biomass loss, decomposition rates, and N dynamics to compare red alder and Douglas-fir litter decomposition over a 2 year period. Based on the traditional understanding of the factors governing the rate of decomposition, I expected that red alder litter would decompose and mineralize N more rapidly than Douglas-fir based on assumptions that litter with more N and less lignin (e.g,. red alder litter) would decompose more rapidly than litter with less N and more lignin (e.g., Douglas-fir litter). I also expected higher N availability at N-fixing

red alder sites would result in more rapid decomposition of litter than in Douglas-fir sites. Finally, I expected that N fertilization of Douglas-fir plots would also increase decomposition rates, mimicking rates under red alder, particularly if N is the driving decomposition regulating factor.

Chapter 3 of this thesis evaluates decomposition of 8 different Douglas-fir foliar litter sources that differ in initial chemical composition, particularly initial N. Of the eight litter sources examined, I expected Douglas-fir litter with higher initial N to decompose more rapidly than Douglas-fir litter with lower initial N. I also expected higher N availability at N-fixing red alder sites would result in more rapid decomposition of litter in red alder than in Douglas-fir sites. Similarly, N fertilization of Douglas-fir riparian sites was expected to stimulate rates of litter decomposition, particularly for the N-poor Douglas-fir litters.

Overall, this study was designed to examine the influence of leaf litter quality characteristics and decomposition site treatment on decomposition rates, to provide a better understanding of how vegetation management can impact nutritional subsidies and nutrient cycles within these riparian systems. Given the critical role that riparian vegetation plays in subsidizing riparian food chains, a key objective of this study was to evaluate decomposition and nutrient cycling of two of the Oregon Coast Range's key riparian tree species to inform management decisions. These experiments will add to growing knowledge of the biogeochemical cycles of different riparian communities and how the quality of the litter and the environmental characteristics interact to influence rate of litter breakdown. This research will further our understanding of the

patterns and the controls of leaf litter decomposition, providing new information on the consequences of converting riparian stands from red alder to Douglas-fir in the Oregon Coast Range.

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CHAPTER TWO - LEAF LITTER DECOMPOSITION IN RIPARIAN FORESTS OF OREGON'S COAST RANGE: A COMPARISON OF RED ALDER AND DOUGLAS-FIR

Introduction

Decomposition of leaf litter plays a vital role in riparian area function. In closed-canopy forested headwater areas, both aquatic and terrestrial food webs rely strongly on carbon, energy, and nutrients derived from riparian forests (Fisher and Likens 1973, Abee and Lavender 1972, Hart 2006). Much of this subsidy occurs via detrital inputs of senesced leaf litter falling onto riparian soils and/or directly into streams (Fisher and Likens 1973). Compositional attributes of riparian forests that are reflected as inter-specific differences in leaf litter chemical quality may therefore influence detrital subsidies to riparian food webs.

Forests of the Oregon Coast Range harbor a wide compositional range of deciduous and evergreen tree species that vary in their nutritional and energetic makeup. This variation may influence their ability to provide nutritional subsidies to riparian food webs. Red alder (*Alnus rubra)* and Douglas-fir *(Pseudotsuga menziesii)* are the two most common early-seral riparian tree species in the Pacific Northwest, and differ in ways important for food web subsidies. Red alder is a deciduous nitrogen-fixing species that provides high N content litterfall in a concentrated autumn pulse, whereas Douglas-fir is an evergreen coniferous species with highly variable N content and only modest seasonality in litterfall dynamics in Coast Range riparian forests (Hart 2006). Nitrogen fixation by red alder also results in higher soil N availability than in corresponding Douglas-fir dominated forests (Binkley 1983, Scott 2004). This may further influence the nutritional quality and incorporation of fallen

litter into detrital food webs. In this way, riparian forests dominated by red alder or Douglas-fir have the potential to differentially influence riparian food web subsidies directly by the provision of leaf litterfall of differing chemical quality, and indirectly by shaping the soil environmental conditions of subsequent leaf litter decomposition.

Both red alder and Douglas-fir are early seral species in the Oregon Coast Range, yet red alder is particularly effective at colonizing and rapidly growing in riparian habitats opened by disturbance (Harrington et al. 1994 *in* Hibbs et al. 1994). As a result, red alder has come to dominate large areas of riparian forest in this region in the wake of historical logging practices that removed large coniferous trees (mostly Douglas-fir, Sitka Spruce, western redcedar, and western hemlock) from hillslopes down to the water's edge. Due to concerns over historic losses of in-stream wood and deep shade that are important for maintaining high quality salmonid habitat, many forest managers in western Oregon encourage the conversion of forests dominated by red alder to forests dominated by conifers. While favoring conifers over red alder may result in long-term improvements to large wood recruitment, conversion effects on leaf litter subsidies that fuel riparian food webs have received very little attention (Volk 2003).

The objective of this study was to examine the decomposition dynamics of red alder and Douglas-fir leaf litter, and evaluate how both species and site influence the rate and temporal pattern of decomposition in Coast Range riparian forests. Based on previous work examining red alder and Douglas-fir decomposition in upland forests of the Pacific Northwest (Fogel and Cromack 1977, Edmonds 1979, Harmon et al. 1990,

Cole et al. 1995, Valachovic 2003), I expect similar findings in riparian areas, i.e. that red alder will initially decompose more rapidly than Douglas-fir due to higher initial litter quality (particularly a lower lignin:N ratio), and that differences in decomposition rates will decrease after about 2 years. I also expect that Douglas-fir litter with higher initial N content will decompose more rapidly than Douglas-fir litter with lower initial N. Further, I anticipate that decomposition rates will be faster at red alder sites than at Douglas-fir sites due largely to higher N availability in red alder versus Douglas-fir sites. Similarly, N fertilization of Douglas-fir riparian sites is expected to stimulate rates of litter decomposition, particularly for the N-poor Douglas-fir litter.

Methods

Study Area

Study sites for this research are located in the Alsea and Siuslaw watersheds of the Oregon Coast Range (44^{o}19'N, 123^{o}30'W) in the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1988). Major coniferous forest species in this area include western hemlock, western red cedar (*Thuja plicata*), and Douglas-fir (Franklin and Dyrness 1988). Because large areas of these Coast Range forests are managed for commercial production of Douglas-fir, stands in this zone are often dominated by sub-climax Douglas-fir forests. Red alder dominates most of the riparian broadleaf stands, and bigleaf maple (*Acer macrophyllum*) is also found throughout Coast Range riparian forests (Pabst and Spies 1999, Nierenberg and Hibbs

2000). Moderated by its proximity to the Pacific Ocean, the maritime climate of the Oregon Coast Range is characterized by cool, wet winters and warm, dry summers. Mean annual temperature averages 10^{o}C. Annual precipitation averages 180 cm and ranges from 150 to 300 cm. Precipitation occurs primarily as rain, falling from October to April. Bedrock across the Coast Range is composed primarily of marine-derived sandstone and basaltic volcanic rock, leading primarily to development of Inceptisols and Andisols (2004 NRCS survey).

Sites chosen for decomposition experiments were selected from sites used in a previous study of stable isotope patterns in red alder and Douglas-fir riparian forests (see Scott et al. 2008 for detailed description) in the central and southern Coast Range (Figure 2.1 and Table 2.1). All sites are located between 15 and 75 km from the Pacific Ocean ranging 80 km north to south. Sites were located in riparian terrace forests dominated by either Douglas-fir or red alder overstory along unconstrained reaches of 2nd to 4th order streams. At Douglas-fir-dominated sites, tree ages ranged from 40-100 years across stands. Western redcedar and western hemlock were also present, with red alder found immediately along stream banks, but only isolated red alder was observed upslope of any Douglas-fir site. At red alder-dominated riparian forests, trees ranged from 30-60 years in age. Bigleaf maple and conifers including Douglas-fir, western red cedar, and western hemlock were also scattered around red alder sites.

This experiment was designed to examine decomposition dynamics of red alder and Douglas-fir litter and the effects of overstory dominance (litter decomposing

in plots under red alder overstory, in unfertilized plots under Douglas-fir overstory, and in fertilized plots under Douglas-fir overstory). Both the litter sources and site treatments varied widely in N availability allowing me to examine the effects of litter source (red alder and Douglas-fir) and external N (N availability in decomposition environment) on decomposition. Eight riparian forest study sites were established for decomposition experiments in November 2003; four sites had overstories dominated by mature red alder and four by Douglas-fir (see Scott et al. 2008). At each red alder site, three 5x5m plots were established in random locations within 50 m of the stream. At each Douglas-fir site, six 5x5 meter plots were randomly located within 50 m of the stream, three of which were fertilized monthly for two years with nitrogen in quantities similar to that fixed by red alder (total 150 kg N ha^{-1} y^{-1}, with half as ammonium nitrate and half as urea) (Binkley et al. 1994). The fertilized plots were scatted randomly among unfertilized plots, but never upslope of or within 5m of an unfertilized plot.

To support assumptions about site nutrient availability, I examined site characteristics and present the results in this section's reference material. In autumn 2004, 9 months after plot establishment and the initiation of fertilization, I sampled litterfall, forest floor, and surface mineral soil (0-10 cm) to evaluate potential differences in N availability and other soil characteristics between unfertilized and fertilized plots under Douglas-fir overstory and in plots under red alder overstory (Table 2.2). Litterfall N concentrations in Douglas-fir needles were nearly twice as high in red alder as in unfertilized Douglas-fir dominated sites (sampled > 20 m away

from N fertilized plots), contributing to significantly lower C:N ratios under red alder in soil and forest floor. Forest floor %N was significantly higher in red alder sites, but did not differ between unfertilized versus fertilized Douglas-fir plots. Red alder mineral soil had significantly lower C:N than either unfertilized or fertilized Douglas-fir soil, but there was no difference in soil C:N between fertilized and unfertilized Douglas-fir plots. Available inorganic N (2M KCl extractable ammonium (NH_4^+) plus nitrate (NO_3^-)) in forest floor was highest in fertilized Douglas-fir plots and lowest in unfertilized Douglas-fir plots. Soil $\%NO_3^-$ differed among all treatments with the highest in red alder soils and lowest in unfertilized Douglas-fir soils. Laboratory potential rates of N mineralization (28 day incubation at 25 °C and 75% field moisture for forest floor, and 60% water holding capacity for mineral soil) were significantly higher in red alder sites relative to either Douglas-fir treatment. Collectively, these data confirm a general pattern of higher N availability in both N fertilized Douglas-fir plots and in red alder dominated sites when compared to unfertilized Douglas-fir dominated plots. These differences permit evaluating how increases in ambient N availability in both the short-term (N fertilized Douglas-fir plots) and the long-term (red alder plots) affect Douglas-fir and red alder decomposition.

Litter Sources

Douglas-fir leaf litter was collected from two 30-50 year old stands in the Coast Range that represent extreme values of low and high foliar N concentrations (Perakis et al. 2006). The selected range of source litter N concentration represents

natural variation in Douglas-fir foliar N due to soil fertility gradients in Coast Range soils. By shaking trees above exposed tarps at each Douglas-fir source site, I collected fresh leaf needle litter in September and October of 2003, at the time of peak needle abscission (Hart 2006). During this period, freshly fallen red alder litter was also gathered from a single plantation site near Toledo, OR. Fresh litter was air dried and held in paper bags in the laboratory for less than one month at room temperature during the construction of litter decomposition bags.

I measured the decomposition of red alder and Douglas-fir leaf litter using the litterbag method in which pre-weighed material was confined within mesh bags (Bobock et al. 1960). By using a known mass at the beginning of the observation period, this method allows for an integrated estimation of mass loss over time. Changes occurring in the sample are assumed to reflect those occurring in undisturbed litter (Woods and Raison 1982). I constructed 20 x 20 cm litterbags using a 1 mm nylon mesh upper layer and a water permeable, non-mesh nylon bottom layer to contain Douglas-fir needles. Approximately 5 grams of litter was weighed, then placed in a litterbag that was stapled closed (amount varied slightly from one bag to another and was recorded as actual amount placed in the bag). While filling litterbags, sub-samples from each air dried litter source were weighed, oven dried at 65° C for 48 hours, and then reweighed to determine moisture content for the series of bags that was being filled at the time the moisture content subsample was taken (the subsample was taken for each source litter approximately every 20 bags). The moisture (measured as loss in mass) of litter was then subtracted from air-dried mass of the bags

related to the subsample for later calculation of decomposition rates. When bags were deployed to the field, one bag per plot was designated as collection interval zero. This bag was placed in the field along with other bags, then immediately collected to an individual plastic bag, returned to the laboratory, oven dried at 65°C for 48 hours, and reweighed for mass loss during transport. As with the moisture content calculation, this value was subtracted from the initial weight of the litter for the specific subset of litterbags the test bag represented. This step was taken because of the tendency for Douglas-fir needles to work their way out of the litterbag during initial field deployment.

Litterbags were deployed to riparian sites between November 18 and 23, 2003. Replicate litterbags were collected for each source in each overstory or fertilization treatment after 2 weeks, 1 month, 2 months, 4 months, 8 months, 1 year, 1.5 years and 2 years. At each collection, freshly fallen materials and moss growth were removed from individual litterbags. Litterbags were placed in an individual plastic bag to avoid any loss of material during transport. At the assigned collection time, the litterbags were placed in individual paper bags for transport back to the lab, oven dried at 65° C, and then reweighed to determine mass loss.

I determined total percent nitrogen and carbon for both initial litter and remaining litter after each collection using a Costech Elemental Combustion System 4010. At least one in every 8 samples (~13%) was run in duplicate. Initial litter Ca, P, Mg, and K were determined using a flame AAS (atomic absorption spectrophotometer) at Oregon State University. Lignin, cellulose, and acid-digestible

fiber (ADF) were determined for initial litter samples using proximate analysis methods (Goering and Van Soest 1970) at the University of Alaska Soil Laboratory.

Calculation of Litter Decomposition Rates

Because several studies evaluating the decomposition dynamics of red alder and Douglas-fir leaf litter report dramatically different temporal patterns of biomass loss (Harmon et al. 1990, Compton and Cole 2001, Prescott et al. 2004), I evaluated the utility of both single and double exponential models in the estimation of litter decomposition rates for these species. Decomposition rates were calculated using eight collection intervals over a two year period.

Single Exponential Model

I modeled Douglas-fir litter decomposition using a single exponential function to obtain the decomposition constant, k (y^{-1}), which is an integrated measure of the rate of decomposition (Olson 1963). Exponential decomposition models have been extensively used to describe the decomposition of litter in litterbags:

$$W_t / W_i = e^{-kt} \qquad \text{(Equation 1)}$$

where W_i is the initial weight of the litter, W_t is the weight of the litter at time t, and k is the decomposition constant. Litterbag weights at each collection interval were determined as the average mass of replicate litterbags collected from three plots per site treatment. The average proportion of mass remaining at each collection interval was then log transformed and the slope of the regression line for mass versus time was used to estimate k. By forcing the intercept through 1 (to account for 100% of

biomass material at onset of decomposition), I was not able to evaluate fit using R^2. I evaluated fit by comparing estimated *k* values from the forced model and with those from a model that was not forced through 0 at t=0. The difference between these values was less than 5%, providing enough certainty that the single exponential model accurately described the decomposition pattern of Douglas-fir litter.

Double Exponential Model

Although the single exponential decomposition model is the most widely used, the double exponential decomposition model often provides a better description of decomposition patterns for certain litters that exhibit rapid initial decomposition followed by slower late stages of decomposition (Bunnell and Tait 1974, Wieder and Lang 1982, Harmon et al. 1990). Graphical analysis of red alder decomposition using the single exponential model revealed poor fit to the data, so a double exponential model was applied. The double exponential model assumes that the substrate is heterogeneous (Minderman 1968, Bunnell and Tait 1974), with two concurrently decomposing pools, one that decomposes rapidly and the other composed of material that decomposes more slowly. The double exponential model is:

$$W_t = W_i(m_f\, e^{-k_f t} + (1 - m_f)\, e^{-k_s t}) \qquad \text{(Equation 2)}$$

where m_f represents the fraction of the initial litter in the fast (i.e., labile) pool, $(1 - m_f)$ represents the slow (i.e., resistant) pool and k_f and k_s are the decomposition constants of the fast and slow pools, respectively. The parameters where determined used non-linear regression.

Two-pool exponential decomposition calculations allow both the pool fractions and their associated *k* values to vary when optimizing model fit. I conducted two sets of calculations using the two-pool model. The first set of calculations used the common approach of an unconstrained two-pool model to calculate optimized pool fractions and associated *k* values. The second set of calculations used a constrained two-pool model that fixed the fast and slow pool fractions equal to their average value across all site treatments, permitting only k_f and k_s to vary in the final model.

"Single exponential equivalent *k*:" An Integrated Measure of Decomposition

In litter decompositions studies, it is assumed that the proportion of remaining mass at time t, y_t, can be described by an exponential model with parameter, *k*, reflecting the constant decomposition rate and α reflecting the initial proportion of mass available, i.e. $y_t = \alpha e^{-kt}$: In most studies, it is reasonable to assume that α=1, or 100% of the biomass is available at time 0. To compare rates of decomposition estimated from different models (single and double component exponential), I calculated an integrated measure of decomposition over the study time frame. I calculate the area between each collection interval by linearly interpolating between collection points, and calculating the area below this line. I then add each of these areas together to form a single integrated measure and from that, I calculate the value of *k* (from the single exponential model) that would result in this area.

One approach to estimating the single exponential equivalent *k* is to linearize this function by taking the $\log_e$ of both sides to give $\log_e(y_t) = \log_e(\alpha) - kt = \alpha' - kt$,

and use least squares or maximum likelihood estimation to solve for α' and *k*. Another approach is to use a numerical approximation. Numerical approximation is based on the area under the curve:

$$A = \int e^{-kt} dt = -e^{-kt} / k \qquad \text{(Equation 3)}$$

Empirically, if decomposition is measured for long enough that remaining mass is essentially 0, then *k* can be estimated as the inverse of the area under the empirical curve:

$$k = 1/\int_0^T e^{-kt} dt = 1/A \qquad \text{(Equation 4)}$$

where T is very large.

If the litter decomposition could be described by a single component exponential decomposition model, the value of the decomposition constant, *k*, that would have resulted in this area after two years can be derived using the following relationship:

$$\int_0^2 e^{-kt} dt = -e^{-kt} / k \,|_0^2 = 1/k - e^{-k2} / k \qquad \text{(Equation 5)}$$

However, in most decomposition studies, litter mass is not measured over a long enough period of time for the remaining mass to be essentially 0, but only over some interval, *I*. In this case, estimates of *k* must be adjusted by a factor depending on both *k* and the area that accounts for the finite measuring period:

$$k = 1/\int_0^I e^{-kt} dt = (1 - e^{-kI}) / A \qquad \text{(Equation 6)}$$

Using numerical approximation by PROC NLIN in SAS, I calculated the area in each successive collection interval by linearly interpolating between collection points and calculating the area below this line as:

$$A = \sum_{i=1}^{I} \left[(t_i - t_{i-1}) * M_i + (t_i - t_{i-1}) * (M_i - M_{i-1}) / 2 \right] \qquad \text{(Equation 7)}$$

where i is the litter bag collection point, i=0, 1, 2,…I; t_i is the amount of time that has passed at collection point i since the litter bags were first put out at time t_0=0, M_i=the proportion of remaining mass in the litter at collection point i.

This integrated measure of decomposition, referred henceforth as single exponential equivalent k_e, is the area under the curves of proportion mass loss versus bag collection time. This value of decomposition, k_e, was developed by Manuela Huso (personal communication, 2007) and can be used as a response variable and comparisons made across litter types and overstory types in the context of this experimental design Because red alder litter loses so much more biomass in the initial stages of decomposition, theoretically its area under the curve is smaller after two years than is that of Douglas-fir and the result is a faster estimated rate of decomposition.

In all subsequent sections, the notation k_e refers to the single exponential equivalent k. The notation k refers to the value calculated using the single exponential model. To describe the fast and slow decomposition rates generated from the double exponential model, the notations k_s and k_f. The notations m_f and m_s were used to describe the proportion of mass in the fast and slow pools.

Statistical Analysis

Because N fertilization plots were included only under Douglas-fir overstory sites and not under red alder overstory which created an unbalanced experimental design, statistical comparisons were made using three separate models. Details of these three models are provided below.

1) *Red alder vs. Douglas-fir Overstory*

To examine the influence of litter source and incubation site on leaf litter decomposition rates, comparisons of red alder and Douglas-fir litter decomposition under red alder overstory and unfertilized plots under Douglas-fir overstories were made using a completely randomized split-plot design.

$$Y_{ijl} = \mu + Overstory_i + \gamma_{j(i)} + Source_l + (Overstory*Source)_{il} + \varepsilon_{ijl}$$

Y_{ijl}	is the mean decomposition rate of the l^{th} litter source in the j^{th} stand in the i^{th} overstory type
μ	is the overall mean value of Y
$Overstory_i$	is the effect of the overstory, i = 1, 2
$Source_l$	is the effect of the lth litter source, l=1, 2, 3
$(Overstory*Source)_{il}$	is the interaction of overstory treatment and litter source.
$\gamma_{j(i)}$	is the error associated with site, that adds variability to the value of Y, $\gamma_{j(i)} \sim N(0,\sigma^2_a)$ This represents the replication within overstory treatment
ε_{ijl}	is the random error term that adds variability to the value of Y; $\varepsilon_{ijl} \sim N(0,\sigma^2)$

2) *Red Alder Overstories vs. Fertilized Douglas-fir Treatment*

To investigate whether any differences in site may be due to higher available N, such as that found under N-fixing red alder, I fertilized three plots within Douglas-fir sites and compared fertilized plots under Douglas-fir overstories to red alder overstories. Like model 1, comparisons of red alder and Douglas-fir litter decomposition under red alder overstories and fertilized plots under Douglas-fir overstories were made using a completely randomized split-plot design. This model was used to test whether or not fertilizing Douglas-fir with N at a rate similar to red alder fixation to Douglas-fir plots would mimic differences in decomposition rates detected between red alder and Douglas-fir treatments.

$Y_{ijl} = \mu + Fert_i + \gamma_{j(i)} + Source_l + (Fert*Source)_{il} + \varepsilon_{ijl}$

μ	is the overall mean value of Y
Y_{ijl}	is the mean value of given response variable
$Fert_i$	is the effect of the fertilization treatment, i = 1, 2
$Source_l$	is the effect of the lth litter source,l=1, 2, 3
$(Fert*Source)_{il}$	is the interaction between fertilization and source litter.
$\gamma_{j(i)}$	is the error associated with fertilization treatment, that adds variability to the value of Y, $\gamma_{j(i)} \sim N(0,\sigma^2_a)$ This represents the replication within fert
ε_{ijl}	is the random error term that adds variability to the value of Y; $\varepsilon_{hij} \sim N(0,\sigma^2)$.

3) *Fertilized versus Unfertilized Douglas-fir plots under Douglas-fir Overstories*

Comparisons of unfertilized to fertilized Douglas-fir overstories were made using a randomized block, split-plot design. This model was used to test whether or

not fertilizing N would increase decomposition in fertilized versus unfertilized plots under Douglas-fir overstories.

$Y_{jkl} = \mu + B_i + Fert_k + \gamma_{j(k)} + Source_l + Fert*Source_{kl} + \varepsilon_{ikl}$

μ	is the overall mean value of Y
Y_{ijl}	is the mean value of given response variable
B_i	is the effect of block, j = 1, 2, 3, 4
$Fert_k$	is the effect of fertilization (i=2), k = 1, 2
$Source_l$	is the effect of the lth litter source, l=1, 2, 3
$(Fert*Source)_{kl}$	is the interaction of fertilization and litter source.
$\gamma_{j(k)}$	is the error associated with fertilization unit, which adds variability to the value of Y, $\gamma j(i) \sim N(0,\sigma^2_a)$.
ε_{jkl}	is the random error term that adds variability to the value of Y; $\varepsilon_{jk} \sim N(0,\sigma^2)$.

Statistical analysis to examine differences in response variable were examined using ANOVA and were performed using SAS v 9.1 statistical software (SAS Institute Inc 2003). Estimate statements were used to evaluate differences in decomposition rates of source litters under a common site treatment and differences in site and fertilization treatment for common litters. A Bonferroni adjustment was made to account for multiple comparisons when examining specific differences among sources and site treatments for biomass loss, the single exponential decomposition equivalent, double exponential parameters, and N mineralization. Using the same design from Models 1, 2, and 3, MANOVA was used to jointly model the effects of design factors on the two decomposition rates estimated in the double exponential models (SAS Proc MIXED procedure). Normal probability plots were examined to evaluate model assumptions. Significance levels were set at $alpha<0.05$ prior to analyses. Because statistical tests were made using the three different statistical models with different

variance assignments, statistical test information is presented in tables, but left out of figures. Standard deviation estimates presented in tables and figures were calculated from raw data for each of the four overstory and fertilization treatments.

Results

Initial Litter Chemistry

Chemical properties measured on initial litter included N, P, Ca, Mg, and K as well as total carbon, acid digestible fiber (ADF), cellulose, lignin, C:N, lignin:N, and the ligno-cellulose index (lignin/(lignin + cellulose))(Table 2.3). Low-N Douglas-fir leaf litter contained 0.68% N. High-N Douglas-fir litter %N was nearly double (1.21%) low-N litter and red alder leaf litter was 2.34 %N. Lignin values were similar between the two Douglas-fir leaf litters (35 and 33% for low-N and high-N Douglas-fir litter respectively), whereas red alder litter lignin was much lower at 9.3%. Red alder litter contained more Mg and K than either Douglas-fir litter source. Both Douglas-fir litter sources contained greater amounts of Ca, ADF, and cellulose than red alder litter. Differences in %N also led to wide disparities in C:N, lignin:N, and ligno-cellulose index among litter sources that were indicative of higher litter quality in red alder than Douglas-fir.

Leaf Litter Decomposition

Decomposition of both low-N and high-N Douglas-fir litters followed a single exponential model with a constant proportion of mass being lost over time. In contrast, red alder leaf litter initially decomposed rapidly followed by a dramatic

decrease in decomposition rate, and so was better described using a double exponential model. The difference in decomposition patterns of Douglas-fir (one pool model) versus red alder (two-pool model) litters made it difficult to perform standard quantitative comparisons of decomposition rates between the species. Therefore, direct comparisons were based on values of single exponential equivalent k_e, calculated from the incremental biomass lost over two years

Biomass Loss

Patterns of biomass loss of the three litter sources (red alder and low-N and high-N Douglas-fir litter) are illustrated in Figure 2.2. This figure highlights differences in the temporal pattern of the decomposition between red alder and Douglas-fir litter sources. Red alder litter lost biomass rapidly for the first 4-6 months, followed by dramatic reduction in mass loss over the rest of the experiment. In contrast, Douglas-fir biomass followed a more constant proportional rate of loss over the 2 year period.

Cumulative mass loss over two years generally occurred in the following order; red alder litter > low-N Douglas-fir litter > high-N Douglas-fir litter (Table 2.4). Across all overstory sites, average mass remaining after 2 years was 46-56% for red alder, 56-65% for low-N Douglas-fir, and 63-69% for high-N Douglas-fir. Litter source significantly influenced mass loss across all overstory types (Table 2.5). Specific differences depended on the litter sources and site overstories considered (Table 2.6). These comparisons were made using a Bonferroni adjustment.

Overall ANOVA comparisons made under model 1 (plots under red alder versus unfertilized plots under Douglas-fir) indicated an interaction between source and overstory ($F_{2,12}$=6.61, p = 0.01, Table 2.5), highlighting the significantly greater mass loss of red alder litter under red alder overstory compared to alder under unfertilized Douglas-fir overstory plots (see Table 2.6 for confidence intervals of specific differences). Low-N Douglas-fir litter lost approximately the same amount of biomass whether under red alder or unfertilized Douglas-fir overstories. In contrast to both red alder and low-N Douglas-fir, there was a trend for high-N Douglas-fir litter to lose more biomass in unfertilized plots under Douglas-fir than under red alder (see Table 2.6 for confidence intervals of specific differences).

Overall ANOVA comparisons under model 2 (plots under red alder versus fertilized plots under Douglas-fir) indicated general differences in mass loss between litter sources, but not site, and there were no site by source interactions ($F_{2,12}$=2.61, p= 0.12, Table 2.5). As under model 1, red alder lost significantly more biomass than both low-N Douglas-fir and high-N Douglas-fir (see Table 2.6 for confidence intervals of specific differences). Low-N Douglas-fir litter also lost more biomass than high-N Douglas-fir (see Table 2.6 for confidence intervals of specific differences).

Overall ANOVA comparisons made using model 3 (unfertilized versus fertilized plots under Douglas-fir) indicated an interaction between source and site treatment ($F_{2,12}$=3.9, p=0.05, Table 2.5, see Table 2.6 for confidence intervals of specific differences). Fertilization of Douglas-fir plots resulted in significantly less mass loss for low-N Douglas-fir litter (see Table 2.6 for confidence intervals of

specific differences) and a trend towards less mass loss for high-N Douglas-fir litter (see Table 2.6 for confidence intervals of specific differences) relative to decomposition of these litters in unfertilized Douglas-fir overstories. Red alder decomposition did not differ significantly when comparing fertilized and unfertilized plots.

Single exponential equivalent k_e

Single exponential equivalent k_e was used to evaluate differences in the temporal rate of decomposition over the 2-year period evaluated in this study (Figure 2.3). Across all sites and fertilization treatments, average k_e was significantly higher for red alder litter (0.51-0.64 yr^{-1}) than for both low-N (0.29-0.31 yr^{-1}) and high–N Douglas-fir litter (0.21-0.22 yr^{-1}) (Tables 2.4, 2.5, and 2.7). Overall ANOVA of k_e showed an interaction between source and overstory treatment under models 1 and 2 ($F_{2,12}$=11.93, p=0.001 for model 1 and $F_{2,12}$=7.89, p=0.007 for model 2, Table 2.5). For comparisons of unfertilized versus fertilized plots, only source was significant ($F_{2,12}$=163.25, p=<0.0001). Under model 1 comparison, red alder litter decomposed much more rapidly under red alder overstories than in unfertilized plots under Douglas-fir overstories (see Table 2.7 for confidence intervals of specific differences). Neither Douglas-fir litter differed when comparing k_e under red alder and unfertilized Douglas-fir plots ($p \geq 0.41$, Table 2.7). Significant interactions in model 2 comparisons revealed significantly more rapid red alder decomposition under red alder overstories than in fertilized plots under Douglas-fir (see Table 2.7 for confidence

intervals of specific differences), but no differences were observed by overstory for either Douglas-fir litter ($p \geq 0.43$). Model 3 comparisons indicated no interaction and no effect of fertilization ($p=0.76$ and $p=0.36$ respectively, Table 2.5), although k_e did differ significantly among source litters in the order red alder > low N Douglas-fir > high N Douglas-fir ($p < 0.001$, Table 2.5).

The Double Exponential Model– Examining Douglas-fir and Red Alder Litter

To compare decomposition of these litters using more traditional comparisons of decomposition rates from exponential models, I compared the parameters from the double exponential model (including the proportion of mass within each pool and the rates associated with these pools (k_{fast} *and* k_{slow}) of 2 Douglas-fir litter sources and red alder litter.

The proportion of mass in the fast pool was larger for red alder litter than either Douglas-fir litter source (Table 2.4). For red alder, the pool size was largest under red alder overstories 31%, followed by fertilized (28%), then unfertilized Douglas-fir (25%). For low-N Douglas-fir, the fast pool was largest (14%) in fertilized plots under Douglas-fir followed by red alder (11%). The fast pool both low- and high-N Douglas-fir was very small in unfertilized plots under Douglas-fir overstories (3% and 2% respectively). Similar, to low-N Douglas-fir the fast pool for high-N Douglas-fir litter was largest in fertilized Douglas-fir treatments (10%) followed by red alder overstory (7%). Generally, the fast pool was larger for red alder litter than either Douglas-fir litter source, and the fast pool was larger both all litter sources under red

alder and in fertilized plots in Douglas-fir, than in unfertilized plots under Douglas-fir (Tables 2.9 and 2.10).

Overall, average fast pool decomposition rate (k_F) across all site treatments ranged from 21 – 38 (y^{-1}) for red alder, 33-122 (y^{-1}) for low-N Douglas-fir, and for high-N Douglas-fir 35-122 (y^{-1}) (Figure 2.4, Table 2.4). Generally, the fast pool was larger for red alder litter than either Douglas-fir litter source, and this pool decayed more slowly than did the smaller fast pool of Douglas-fir (Figure 2.4, Tables 2.11 and 2.12). Across all sites and fertilization treatments, the average slow pool decomposition rate ranged from 0.18-0.24 (y^{-1}) for red alder litter, 0.17-0.28 (y^{-1}) for low-N Douglas-fir, and for high-N Douglas-fir 0.15-0.22 (y^{-1}) (Figure 2.4, Table 2.4). Generally, the slow pool was smaller for red alder litter than either Douglas-fir litter source (Tables 2.13 and 2.14). While rates of the slow pool of red alder litter were faster under red alder and fertilized Douglas-fir than unfertilized Douglas-fir, the trend was reversed for Douglas-fir litters. For both Douglas-fir litter sources, rates of the slow pool were most rapid under unfertilized Douglas-fir treatments, with red alder intermediate, and rates under fertilized Douglas-fir reduced (Table 2.4, 2.13, 2.14).

Evaluating Red Alder Leaf Litter Decomposition Using a Two Pool Model

In the unconstrained double exponential model, the fast pool of red alder litter was largest under red alder overstories (31%, Table 2.4), followed by fertilized Douglas-fir plots (28%) and unfertilized Douglas-fir plots (25%). The decomposition rate of the fast pool varied inversely with the proportion of mass in that pool and was

greatest in unfertilized plots under Douglas-fir overstories (38 y^{-1}), followed by fertilized plots under Douglas-fir overstories (26 y^{-1}), and red alder overstories (21 y^{-1}) (Figure 2.5). In unfertilized Douglas-fir plots, there was a smaller proportion of mass in the fast pool, but this mass decomposed significantly faster than the fast pool decomposed under red alder ($p= 0.02$, Table 2.11, 2.12).

Results from the constrained model (i.e., where fast and slow pool sizes were fixed to the average proportion across all treatments) were similar to that of the unconstrained model, showing no significant differences among the model variables (Table 2.9) under MANOVA. Qualitatively, the most apparent change when looking at the constrained model compared to the unconstrained model was that the decomposition rate of the slow pool increased slightly in fertilized plots under Douglas-fir overstories, and decreased slightly under red alder overstories (compare Figures 2.4 and 2.5 and Table 2.4). Comparisons of variables across models indicate that under red alder, constraining the pool size decreased the proportion of the fast pool from 31% to 28%. This change resulted in an increase of both the slow pool and fast pool (from .24 to 0.27 (y^{-1}) and from 20.6 to 24.3 (y^{-1}) respectively). In unfertilized Douglas-fir plots, constraining the pool size increased the proportion in the fast pool from 25% to 28%. In this case, the rate of slow pool also increased from 0.18 to 0.20 (y^{-1}) and the fast pool was reduced from 38.3 to 30.8 (y^{-1}). In fertilized Douglas-fir plots, the proportion of mass in the fast pool was similar to that from the unconstrained model (28%). In this case, the pool size was constrained at 28% and

there was little change in the rate of the slow pool (0.18 to 0.20 (y^{-1})), but the fast pool decreased (from 27.8 to 20.8 (y^{-1})).

Litter N Dynamics

N dynamics differed markedly among red alder and Douglas-fir litter sources (Figures 2.6 and 2.7 and Tables 2.15 - 2.17). Red alder litter started mineralizing N from the outset of the experiment, and after 2 years contained 31-53% of original N in the various site treatments (Figure 2.6 and Table 2.16). In contrast, %N in low-N Douglas-fir litter increased substantially, ranging from 151 - 180% of initial value, with greatest N immobilization in red alder sites and least N immobilization in unfertilized plots under Douglas-fir overstories (Figure 2.6, Tables 2.15 - 2.17). Overall, high-N Douglas-fir litter immobilized less N than low-N Douglas-fir, ranging from 92-125% of initial N (Figure 2.6, Tables 2.15 - 2.17).

The absolute quantity of N (mg) immobilized per gram of initial litter was also calculated to provide an unbiased estimate of N immobilization that controls for differences in initial %N of source litters (Figure 2.7 and Table 2.16). Examinations of the amount of N (mg) immobilized per gram of initial litter indicate that overall patterns paralleled those of the percent of initial N. ANOVA of N immobilized after two years showed significant differences among litter sources in all comparisons (Tables 2.16 and 2.17), but no effects of site or source by site interactions. After two years, low-N Douglas-fir litter consistently immobilized the most N in all plots, followed by high-N Douglas-fir, and then red alder (Tables 2.16 and 2.17). At the end of 2 years, low-N Douglas-fir litter had immobilized 5.4, 3.4, and 4.2 mg N / g litter

under red alder, unfertilized and fertilized plots under Douglas-fir overstories, respectively. High-N Douglas-fir litter generally immobilized less N than low-N litter, and after 2 years had begun to mineralize N under red alder overstories and in unfertilized plots under Douglas-fir overstories (0.32 and 0.93 mg N / g litter), while continuing to immobilize N under N fertilization (3.1 mg N / g litter). Red alder litter mineralized N under all treatment conditions (16.1, 12.4, and 11.2 mg N / g litter under red alder overstories and in unfertilized and fertilized plots at Douglas-fir overstories, respectively).

Values for C:N of the three litter sources ranged initially from 23-76 (Figure 2.8 and Table 2.10). Temporal changes in C:N ratios differed between Douglas-fir and red alder leaf litter (Figure 2.8). Red alder litter C:N remained relatively constant for most of the 2 year period, except for a slight increase in C:N in the final collection at two years (from 23 to 32 under red alder, 23 to 27 under unfertilized Douglas-fir, and from 23 – 24 under fertilized Douglas-fir). The C:N of low-N Douglas-fir litter showed the most dramatic decrease from 76 to 22 under red alder overstories, 76 to 28 in unfertilized plots under Douglas-fir overstories and from 76 to 30 in fertilized plots under Douglas-fir overstories. High-N Douglas-fir C:N ratios fell from 44 to 31 under red alder overstories, from 44 to 28 in unfertilized plots under Douglas-fir overstories and from 44 to 23 in fertilized plots under Douglas-fir overstories.

Discussion

Influence of Litter Source

This is the first study to report decomposition and nitrogen dynamics of Douglas-fir and red alder leaf litter in riparian forests of the Pacific Northwest. These results generally reinforce previous findings derived from upland forests that show more rapid decomposition of red alder than Douglas-fir litter within 1-3 years (Edmonds 1980, Harmon et al. 1990, Fyles and Fyles 1993, Cole et al. 1995, Valachovic et al. 2004). This study also extends the generality of this finding by showing more rapid decomposition of red alder than Douglas-fir across a nearly 2-fold variation in initial N content of Douglas-fir litter (0.68-1.21% N), variation in the site of decomposition (red alder vs. Douglas-fir sites), and in response to N fertilization (150 kg N ha^{-1} yr^{-1}). A combination of factors is likely responsible for more rapid decomposition of red alder than Douglas-fir litter, including a larger water soluble fraction of mass in red alder, lower lignin content, and higher internal tissue N (Harmon et al. 1990). It is possible that longer-term decomposition beyond the 2 years considered here may have yielded more similar decomposition rates for these two species, as red alder is known to exhibit slower mass loss in the late stages of decomposition (Cole et al. 1995, Prescott 2000).

When contrasting red alder and Douglas-fir, my results were consistent with the traditional understanding of the relationship between litter quality and decomposition rates across species. Red alder with high N and low lignin:N decomposed more rapidly than Douglas-fir litter, especially during the first year of decomposition. However, results contrasting the decomposition of low-N vs. high-N Douglas-fir litter did not fit this traditional paradigm. Instead, low-N Douglas-fir litter

decomposed more rapidly than high-N Douglas-fir litter, possibly due to interference of high N with ligninase enzymes that break down lignin (Fog 1988 and Carreiro et al. 2000, discussed more in Chapter 3). Yet it remains surprising that even the earliest stages of decomposition (i.e., within the first 4-6 months) that are typically dominated by labile C compounds failed to show more rapid decomposition of high-N Douglas-fir litter, suggesting that N may not be limiting to decomposition of Douglas-fir needles in these forests.

Mass loss in red alder, which followed a 2-pool exponential decomposition model, was particularly rapid in the first 6 months. This initial rapid mass loss in red alder is likely attributable to greater content of water soluble material in red alder (15-25% of initial mass) than Douglas-fir (6.7-7.7% of initial mass) (values from Harmon et al. 1990, also shown by Fyles and Fyles, 2003). My deployment of litterbags in November coincided with the onset of seasonal winter rains in the Oregon Coast Range, which would have facilitated rapid loss of water soluble compounds from the litters. Results from the double exponential model for Douglas-fir litter suggest that ambient N can increase the size of the fast pool, since red alder and fertilized Douglas-fir treatments had larger fast pools than in unfertilized plots under Douglas-fir. The resulting differences in decomposition rates of various pool varies across sites. Overall these analyses support research suggesting that N affects decomposition in different ways depending on both internal factors (e.g. whether N stimulates decomposition of cellulose or suppresses the decomposition of lignin) and external

factors (e.g., whether the ambient nitrogen is naturally or artificially derived, Knorr et al. 2005).

Approximately 70% of red alder litter mass on average was attributed mathematically to slow pool kinetics (Table 2.4). This calculated slow pool in red alder decomposed more slowly than either Douglas-fir litter source overall. This difference suggests that the greater potential subsidy provided by red alder to riparian food webs may be short-lived and only applicable to the most labile litter components that decompose rapidly in red alder. Though I did not measure lignin in decomposing litter, it is possible that the relative proportions of N and lignin for high-N Douglas-fir litter and the slow pool of red alder are more comparable to one another than to low-N Douglas-fir. The difference observed in slow-pool decomposition of red alder when compared to low-N vs. high-N Douglas-fir provides indirect evidence that variations in Douglas-fir litter quality resulting from legacy N fixed by red alder may have subtle long-term effects on detrital-based food webs.

Several lines of evidence in my study suggest that litter decomposition rates, particularly for red alder, depend on the decomposition environment. I detected a significant interaction between litter source and decomposition environment characterized by greater mass loss of red alder when decomposed in red alder than in Douglas-fir sites. Because N fertilization of Douglas-fir plots did not increase red alder decomposition relative to unfertilized plots, it seems unlikely that the faster overall decomposition of red alder in red alder sites is due to high N status in red alder sites. The 2-pool decomposition parameters for red alder litter decomposition also

revealed a slightly larger proportion of mass in the “fast” pool when red alder litter was decomposed under red alder overstories (31% of total mass) than Douglas-fir (25 - 28%). One plausible explanation for this phenomenon is that the soil fauna (those small enough to pass through the mesh bags) and microbial community associated with red alder is better able to utilize a larger proportion of the mass early in decomposition. Alternatively, the loss of red alder canopy foliage in autumn due to leaf abscission may have promoted greater leaching of soluble compounds from red alder in red alder sites because of more direct throughfall. Regardless of the mechanism, the synergistic effect of more rapidly decomposing red alder leaves in red alder habitats may make energy and nutrients more rapidly available to biotic communities under red alder, and thus influence local food web dynamics.

There is long-standing interest in understanding interactions between red alder and Douglas-fir in the Pacific Northwest (Binkley 1993, Radosevich et al. 2006). The two species often co-occur early in succession in moist coastal forests, and are also planted together in managed stands. Mixtures of the two species have been explored extensively as a means of using N fixed by red alder to improve Douglas-fir growth and nutrition (Hibbs et al. 1994), but our ability to infer effects on other ecosystem processes from these studies is limited. My results support the idea that red alder can improve Douglas-fir nutrition and litter quality, measured as significantly higher foliar N of litter produced by Douglas-fir when grown in red alder than Douglas-fir dominated stands (1.3 vs. 0.8 foliar %N, Table 2.2). However, this improvement in litter quality does not appear to stimulate Douglas-fir decomposition, as I found that

high-N Douglas-fir litter decomposed more slowly than low-N Douglas-fir litter. This result is part of a broader negative relationship between foliar %N and decomposition rate observed in Douglas-fir (Chapter 3).

My results also indicate that red alder did not influence Douglas-fir decomposition at the site level. Decomposition rates of Douglas-fir did not differ in red alder sites vs. unfertilized Douglas-fir sites for either high-N or low-N litter (Table 2.7, Model 1). In contrast, Prescott et al. 2000 found marginal evidence that between 0.5 to 1.5 years, both Douglas-fir litter and red alder litter decomposed more rapidly in red alder plots, but differences did not persist after 3 years of decomposition. They suggest that the more rapid decomposition under red alder could have been related to more active soil fauna under broadleaf forests (Killham 1994, Anderson 1988). Differences in methods of calculating decomposition rates in the current study (single exponential equivalent k_e) versus Prescott et al. 2000 (single exponential model) may have also shaped the differences observed in these two studies. Although red alder can clearly have a beneficial influence on the growth and nutrition of Douglas-fir, it is less clear that such effects can be readily transferred to understand how red alder influences Douglas-fir detrital dynamics.

The Influence of Overstory and Fertilization on Decomposition

My results suggest site factors can also play an important role in decomposition dynamics. I evaluated decomposition at sites under N-fixing red alder overstories and in unfertilized and fertilized plots under Douglas-fir overstories. Based on the assumption that N limits microbial decomposition, this design enabled

me to evaluate if site N availability can regulate decomposition. In addition to my hypothesis that decomposition rates would be more rapid in N-rich red alder sites versus comparatively N-poor Douglas-fir sites (Table 2.2), I also expected that fertilizing Douglas-fir sites with N would increase rates of decomposition similar to those observed under red alder overstories.

Contrary to my expectations, N fertilization had either neutral or negative effects on decomposition rates. Although single exponential equivalent *k* in Douglas-fir litters did not change with N fertilization, I found that N fertilization was associated with 9% less mass loss than under unfertilized conditions after two years in low-N Douglas-fir litter ($p = 0.007$) and 15% less mass loss in high-N Douglas-fir litter ($p = 0.09$) (see Chapter 3). This potential N inhibition of decomposition of lignin-rich Douglas-fir litter is consistent with the idea that excess supply of N inhibits the ligninase enzyme production that is critical for lignin breakdown (Berg 1986, Fog 1988).

Overall, I found only partial support for the idea that differences in decomposition between red alder and Douglas-fir riparian areas was related to N as a driving mechanism. Fast pool dynamics in red alder were slowed by N fertilization to rates more similar to that observed under red alder, and mass remaining after 2 years in high-N Douglas-fir litter was lower in both N fertilized and red alder sites compared to unfertilized plots. On the other hand, single exponential equivalent k_e and mass remaining indicated significantly faster decomposition of red alder litter under red

alder than under fertilized Douglas-fir overstories, supporting the idea that factors other than N may be important for red alder decomposition.

Factors related to microbial community activity can also play an important role in decomposition dynamics. While I did not measure microbial community activity, it is likely that the rapid decomposition of red alder litter under red alder could be due in part to the activity of the decomposer community. Hunt et al. (1988) suggested that the nature of microorganisms and soil fauna active in the decomposition process can regulate decomposition. Staaf (1987) observed that mass loss of beech litter was positively correlated with the nutrient status of soil and suggested that the increased mass loss could be attributed to site conditions that favored microbial and microfaunal turnover. Schaefer and Schanuerman (1990) reported higher decomposer biomass and species diversity in nutrient rich sites. This could also have contributed to the interaction I observed between litter source and site, at least for red alder litter decomposing at red alder sites (see subsequent section). Given the diversity of soil ecosystems and decomposer fauna, it is plausible that any of these factors may ultimately regulate decomposition at a particular site.

Source and Overstory Treatment Interactions

Regardless of which measure was used to evaluate decomposition, red alder decomposed more rapidly than either Douglas-fir litter source, and its decomposition was most rapid under red alder overstories. N fertilization failed to stimulate red alder decomposition, and even appeared to inhibit decomposition of the fast pool. Therefore, I speculate that red alder litter decomposition is more rapid under red alder

than Douglas-fir overstories because either the microbial community under red alder is well adapted to decompose red alder litter and/or the open canopy conditions of red alder outside the growing season facilitates red alder decomposition. Throughfall and leaching may be greater in the absence of a canopy during late fall, winter and early spring, thus facilitating leaching of materials from red alder. An alternative explanation is UV light that has been shown to be powerful in aiding decomposition in arid environments (Austin and Vivanco 2006), and may be important in deciduous forests as well, although this effect would be attenuated in the winter months at high latitudes. Conversely, Douglas-fir litter decomposition did not differ when comparing red alder sites to unfertilized plots under Douglas-fir. For high-N Douglas-fir litter, biomass loss was greater in unfertilized plots under Douglas-fir overstories than under red alder overstories or in fertilized plots under Douglas-fir overstories, contrary to the expectation that increasing N would increase decomposition.

Vesterdal (1999) evaluated the effect of site differences based on site nutrient availability of both Norway spruce (*Picea Abies*) and beech (*Fagus sylvatica*). He found that variations in site nutrient availability increased beech decomposition rates, but had no effect on decomposition rate of Norway Spruce. He suggested that aspects of site nutrient availability can affect different species in different ways, and that decomposition of a particular species at a particular site is controlled by the factor that is most critical to the decomposer organisms. He attributed the differences to site and soil properties having different effects on different species. Evaluating decomposition

data generated from the single exponential model after 4 years of decomposition, Prescott et al. (2004) found no evidence of an interaction between litter source and decomposition, reporting that both red alder and Douglas-fir litter decomposed faster in red alder sites than in Douglas-fir sites after 6 years. It is possible that when we examine the litter decomposition from this study after 4 years, our marginal evidence for the source by site interaction will no longer be apparent because differences in decomposition rates will not persist into later stages (with similar overall biomass loss in later stages of decomposition).

Several other studies have also examined whether a particular litter decomposes more rapidly in its system of origin. Bocock and Gilbert (1957) found no interaction between litter type and site. In contrast, Hunt et al. (1988) found that decomposition of a particular litter was faster when placed in its system of origin. They argued that this interaction suggests that decomposers in a particular ecosystem are adapted to the most prevalent type of litter and that substrate quality by itself is insufficient for predicting decomposition of a particular litter and that decomposition can vary by habitat and change over time within an ecosystem.

Altogether, results from this study and others suggest that substrate quality alone is insufficient for predicting decomposition of a particular litter and that decomposition of a common litter can vary depending on the site conditions in which it is decomposing. These results underscore the need to recognize the differences among litter species in decomposition dynamics, and how differences in litter quality factors can respond to environmental N in different ways.

Red Alder Decomposition Dynamics –Evaluating the Utility of the Two Pool Model

While Douglas-fir litter decomposition can be adequately described using a single exponential model, the use of a model assuming a single rate of decomposition does not describe the decomposition dynamics of red alder litter. Harmon et al. (1990) observed that red alder litter decomposed slower than as predicted by the single exponential model, indicating that as decomposition progressed, the influence of dramatic decline in decomposition in later stages was not accounted for by the single exponential model. The single exponential model can be particularly misleading for species like red alder because the results can vary dramatically depending upon the length of the incubation period. To better capture the decomposition dynamics of red alder, I employed the double exponential model as described by Bunnell and Tait (1974). This model divides the litter into two distinct proportions—one that decompositions very rapidly early in decomposition, and the other that decompositions much more slowly and so persists into later stages. Employing the double exponential model, I was able to evaluate whether site influenced the size and rate of these relative proportions. The two pool model produced a rate of decomposition for both the fast and slow pools. These values bracket the values obtained from the single exponential equivalent *k* (k_e) rate, thus providing insight into both the rate and pattern, or temporal pattern, of red alder decomposition.

The results suggested that under red alder overstories, the relative size of the fast pool is larger, and its rate slower than that of the comparable, smaller fast pool which decomposes more rapidly in unfertilized plots under Douglas-fir overstories.

This implies that the size of the easily accessible pool, the fast pool, is larger when decomposing under red alder overstories (i.e. proportion affects the decomposition rates values, so when comparing parameters in the two pool unconstrained model, one needs to look at both the proportion and the decomposition values).

Results also show that N fertilization slowed the fast pool decomposition in red alder. This was observable even though overall effects of N on alder decomposition for both k_e and mass remaining were not strong. However, neither red alder k_e nor mass remaining after 2 years were altered significantly by N fertilization, suggesting that any overall potential inhibitory effect of added N on red alder dynamics was probably slight and relatively short-lived in the context of this 2 year study. N fertilization did not affect decomposition of the slow pool in red alder as calculated by the unconstrained model, although this result may depend in part on parameter estimation in the model itself.

While Bunnell and Tait (1977) argue it is important to predetermine the mass proportions (using chemical analysis), others have run the model using the biomass data to determine both the decomposition rates and relative proportion in each pool (Harmon et al. 1990). In this analysis, I started by allowing the model to estimate all the model parameters (similar to Harmon et al. 1990). These results from the unconstrained model where then used to help determine the mass proportion for a separate run of the double exponential model where the pool size was predefined. To determine this proportion, I took the average value calculated across all the different treatments from the unconstrained model. Results from the unconstrained model

indicate that the pool size is larger for red alder litter when it is decomposing under red alder overstories, but that this rate of decomposition is slower than that of red alder decomposing under Douglas-fir overstories. That is, there is more in the fast pool under red alder than under Douglas-fir, but the relatively smaller pool decomposing under Douglas-fir is decomposing more rapidly that the fast pool decompositions under red alder overstories. When the pool size is constrained, the decomposition of the fast pool under red alder is reduced under both red alder and Douglas-fir overstories, however, the magnitude of reduction is greater under Douglas-fir overstories.

Overall, this analysis demonstrated that setting the mass proportion in constrained analyses gives some expected changes in the rates of decomposition of the two pools, and that this may be a mathematical inevitability. Results suggest that as proportion in the fast pool gets smaller, its rate increases. The rate of the slow pool is also affected, but the magnitude is much smaller. When the fast pool size was increased or remained relatively constant, its rate decreased. Alternatively, when the proportion of the slow pool increased, the rate of decomposition of the slow pool also increased. When the proportion of the slow pool decreased, the rate of the slow pool decreased. When the proportion of the pool size was fixed at 28%, the rate of the slow pool did not change. Due to the small sample size and high variability of the modeling exercise, it is difficult to determine whether these are biological effects or a mathematical artifact of manipulating the model parameters.

N Cycling

Litter quality plays an integral role in decomposition dynamics and can also influence the rate of nutrient mineralization (i.e., nutrient release from litter). While the pattern of mineralization varies by species (Melillo et al. 1982), the process eventually results in a net reduction in the amount of nutrients held in the litter. To support their growth and in turn fuel the decomposition process, microbes need a combination of energy (various C compounds) and nutrients (particularly N and P). While some nutrients are contained within the decomposing litter, microbes must often draw in additional nutrients from their environment through fungal hyphae, throughfall, and fixation to build microbial biomass (Aber et al. 1991). Early in decomposition, carbon is more readily available, making it more likely for nutrients such as N to be limiting. Later in decomposition, after microbes have metabolized easily accessible carbon and drawn in or immobilized nutrients from the external environment, the complexity of the remaining carbon molecules plays an increasingly dominant role in the decomposition of the remaining recalcitrant material (Aber and Mellilo 1990, Hobbie and Vitousek 2000). In comparisons of beech and Norway spruce, Vesterdal (1999) found that initial nutrient quality played a larger role in nutrient release than did nutrients in soil or forest floor. McClaugherty et al. (1985) suggested that during early phases of decomposition, initial litter quality regulates nutrient release, but that during later stages of decomposition, the importance of the soil environment may increase.

The pattern of N dynamics that I observed in decomposing litter differed dramatically for red alder and Douglas-fir. Consistent with Edmonds (1980), red alder

mineralized N from the onset of decomposition, continuing over the two year period examined. In contrast, both low-N and high-N Douglas-fir litter showed pronounced N immobilization throughout much of the experiment. Relative to the initial %N, low-N litter immobilized more N than high-N litter in every treatment, presumably reflecting differences in N available in the decomposing substrate (Prescott 2005, Vesterdal 1999). Despite little difference in biomass loss (for a species) relative to site (red alder versus Douglas-fir sites), a greater percentage of N was immobilized in red alder sites suggesting that site can influence both the quantity and the temporal pattern of N mineralization. Greater N immobilization under red alder overstories and in fertilized plots under Douglas-fir overstories may reflect luxury uptake by some microbes, while inhibiting lignolytic enzyme production by others.

N mineralization has also been related to biomass loss. Howard and Howard (1974) report N immobilization or accumulation phase lasting until approximately 35% mass loss. Staaf and Berg (1977) also reported that the immobilization phase for Scots pine phase ended after 35% mass loss. In this study, low-N Douglas-fir biomass loss was 44%, 43%, and 23% for red alder sites, Douglas-fir sites, and fertilized Douglas-fir plots respectively, suggesting that biomass alone does not determine N mineralization. Regardless of treatment, low-N Douglas-fir continued to immobilize N under all site treatments until the end of the experiment. For high-N Douglas-fir, biomass loss was 33%, 36%, and 30% for red alder sites, unfertilized plots under Douglas-fir overstories, and fertilized plots under Douglas-fir overstories respectively. High-N Douglas-fir N mineralization had begun to occur in unfertilized plots under

Douglas-fir overstories, which had the greatest mass loss, just over 35%, but was still immobilizing N under red alder overstories and in fertilized plots under Douglas-fir overstories. These results suggest that biomass loss may influence N mineralization, but that biomass loss alone does not determine N mineralization rates for Douglas-fir litter. Red alder litter mineralized N from the onset of decomposition, suggesting that for extremely N rich litter, biomass loss plays little role in N mineralization.

N mineralization has also been related to changes in the C:N of decomposing litter and the relationship between the C:N ratio and N mineralization and has been shown to vary depending on decomposition site (Berg and Ekbom 1983). While some studies have suggested that there is a fixed C:N ratio of 25 at which net release occurs (e.g. Mulder et al. 1969), Berg and Laskowski (2006) argue there is very little experimental evidence to support this generalization. Instead, they argue there are several phases for N dynamics and that these are not directly related to a steady decline in C:N. Consistent with Edmonds (1980), I found that litter with lower C:N ratios (red alder leaf litter) decomposed more rapidly early in decomposition than either sources of Douglas-fir litter with higher C:N ratios. Over the course of 2 years, the differences between these ratios decreased as carbon was consumed and N was either mineralized (red alder litter) or immobilized (both Douglas-fir litter sources). Edmonds (1980) found that the C:N ratio for red alder fell from 31.5 to 19.6, then remained constant. In contrast, the C:N ratio of red alder litter in this study actually

rose from 23 to between 32, 27, and 24 at red alder sites and in unfertilized and fertilized plots, respectively.

For low-N Douglas-fir, the C:N ratio showed the greatest decline (76 to 22, 28, and 30 at red alder sites and in unfertilized and fertilized plots under Douglas-fir). High-N Douglas-fir showed less of a decline than low-N Douglas-fir starting at 44 and ending at 31, 28, and 24 under red alder overstories and in unfertilized and fertilized plots under Douglas-fir overstories. The differences in the final C:N for the two Douglas-fir litter sources suggest that both the initial C:N in the litter and the site treatment can influence the final value. In unfertilized plots under Douglas-fir, both litter sources had a value of 28. This suggests that low-N Douglas-fir litter is drawing more N into the decomposing litter, and losing biomass more rapidly. It also suggests that under unfertilized Douglas-fir, litter sources tend to converge at a similar C:N value despite initial differences in litter quality and decomposition rates. However, Figures 2.6 and 2.7 suggest that the N release and accumulation fluctuates over time. This is consistent with Berg and Laskowski (2006) who propose that N dynamics vary over time depending on the stage of decomposition. After 2 years, C:N ratios ranged from 22-32 with no apparent relationship to net release, at least across all litter sources examined. However, under red alder overstories and in fertilized plots under Douglas-fir overstories, which both have higher available N in forest floor and soil, values between the two Douglas-fir litter sources diverged. Under red alder, C:N of low-N Douglas-fir litter was lower than high-N Douglas-fir (22 and 31, respectively). In fertilized plots under Douglas-fir, low-N Douglas-fir was higher than high-N Douglas-

fir (30 and 23, respectively). This suggests that both litter quality and site characteristics may influence N mineralization and that the nature of external N availability (natural or fertilized) can affect N mineralization from litter in different ways.

Several scientists have argued for a close functional relationship between litter quality, decomposition rates, and site productivity, which interact resulting in a positive feedback cycle that can either promote or inhibit nutrient cycling (Gosz 1981, Vitousek 1982). This theory suggests that leaf litter of high quality decomposes rapidly, mineralizing carbon and nutrients, leading to high soil productivity, high nutrient uptake, and nutrient rich litter which in turn, decomposes rapidly (Gosz 1981, Edmonds 1980). During the early phases of decomposition, the rapid biomass loss of red alder supports the idea of a positive feedback mechanism between high quality, rapid decomposition, and high site productivity. Studies in the Coast Range have shown that a diverse array of fauna are often most abundant in red alder dominated habitats, presumably due to the greater nutritional quality of red alder litter and associated plant species (Miller 1986). Conversely, litter of lower initial quality (higher lignin:N) such as Douglas-fir needles decomposes more slowly, which can lead to slower nutrient cycling rates and lower soil fertility (Aber and Melillo 1982, Mellillo et al. 1982, Berg and McClaugherty 1989, Aber et al. 1990, Harmon et al. 1990, Hobbie 2000, Prescott et al. 2000, Vitousek 1982). As a result, slowly decomposing litter leads to slower rates of energy and nutrient release (Gosz 1981).

Management Implications

In the Oregon Coast Range, riparian areas are often dominated by coniferous species such as Douglas-fir, or by the pioneering deciduous hardwood red alder. Douglas-fir riparian forests provide year round shade and contribute to in-stream complexity through the input of decomposition resistant large woody debris (LWD) (Pabst and Spies 1998). Given the critical role that riparian vegetation plays in subsidizing the productivity of riparian food chains, there is a risk that riparian management strategies (specifically conversion of red alder riparian stands with coniferous ones) based solely on large wood and shade needs may be creating a new set of problems, a new set of limiting conditions in Coast Range streams. Intuitively, it makes sense to balance large wood and shade needs with the nutritional values provided by riparian vegetation, especially N-rich red alder litter. While my study did not examine differences between Douglas-fir and red alder in terms of providing large wood and shade, they do suggest that red alder is an important component of healthy riparian systems because it provides energy and nutrients. It is clear from studies of insect and animal populations that diversity and abundance is higher under red alder overstories than under Douglas-fir (Miller 1986).

Douglas-fir needle litter is relatively resistant to decomposition with high concentrations of lignin and low concentrations of N. Red alder, which fixes N, contains litter N concentrations two to three times higher than Douglas-fir (Abee and Lavender 1972, Valachovic et al. 2004, Volk et al. 2003, Scott 2004). Binkley et al. (1992) found that the return of nitrogen to the soil in the form of litterfall in alder-conifer stands was as much as 7 times greater than coniferous stands. Additionally,

red alder can also increase soil C in part due to its productivity relative to Douglas-fir (Cole et al. 1995).

Several researchers have evaluated differences in a broad array of characteristics between broadleaf species (such as red alder) and coniferous species (such as Douglas-fir) (Prescott et al. 2000, Perry et al. 1987). Among the perceived benefits of broadleaf species is rapid decomposition and mineralization of leaf litter, both of which can result in faster nutrient cycling and enhanced productivity (Perry et al. 1987). Additionally, forest floor turnover has been estimated to occur four times faster in temperate broadleaf than in coniferous forests, with deciduous species also contributing higher base cation concentrations and thus forest floors with higher base cation availability and pH (Binkley and Valentine 1991). Binkley (1983) also found greater soil carbon and nitrogen content, and N availability and greater total net primary productivity where red alder was present in Douglas-fir sites.

The decomposition of senesced leaf litter and the subsequent release of carbon and nutrients provide much of the energetic base of food chains in riparian forests. While this study did not observe sustained levels of rapid decomposition of red alder, N-rich red alder mineralized N from the onset of decomposition, suggesting that red alder litter plays an extremely important role in supplying N to the system. As senesced red alder leaves fall, nearly 20% of their mass is lost (some of which is likely a result of physical leaching) to the surrounding environment in the first two weeks of decomposition leading to an immediate net release of N (Hart 2006). Though Douglas-fir needle senescence does increase in response to moisture stresses,

particularly in late summer and fall, leaf litter reaches the forest floor throughout the year. Once on the forest floor, Douglas-fir needles lose biomass at a relatively constant rate, but continue to immobilize N throughout the first two years of decomposition. This slows release of N to the system to support plant growth. The rapid decomposition of red alder litter and mineralization of N may promote the transfer of nutritional subsidies from vegetation to terrestrial detrital food webs (Hart 2006).

Conclusions

The objectives of this chapter were to examine the decomposition dynamics of red alder and Douglas-fir leaf litter and evaluate how both species and site influence the rate and temporal pattern of decomposition in Coast Range riparian forests. I experimentally examined how differences between red alder and Douglas-fir leaf litter and certain site characteristics influence decomposition dynamics. Overall, broad decomposition patterns of red alder and Douglas-fir leaf litter followed expected trends with higher quality red alder litter decomposing more rapidly than lower quality Douglas-fir litter. Red alder litter decomposed very rapidly in early stages of decomposition followed by a dramatic decrease in mass loss. The rapid decomposition of red alder litter was especially pronounced in red alder sites. However, after the fast pool of red alder litter had decomposed, the remaining proportion decomposed more slowly than Douglas-fir litters. By contrast, both Douglas-fir litter sources decomposed more slowly from the onset of decomposition following the single exponential pattern which has been used extensively to model

decomposition. The surprisingly rapid decomposition of low-N relative to high-N Douglas-fir needles suggests that internal N content does not limit decomposition in this species, in these systems. Reduced rates of decomposition of Douglas-fir litter in fertilized plots under Douglas-fir overstories further suggests that N may actually slow decomposition, particularly for high-N litter. This analysis is explored in greater detail in the companion study (Chapter 3).

N dynamics were also markedly different when compared across species. Red alder litter N was released from decomposing litter from the onset of decomposition indicating that there is sufficient N contained within the litter substrate to meet microbial demand. In contrast, both Douglas-fir litters immobilized N throughout the 2 year period in all but one case. High-N Douglas-fir litter began mineralizing N in unfertilized Douglas-fir sites between 1.5 and 2 years. This suggests that greater N availability in the decomposition environment may actually slow rates of N mineralization at these sites by locking it up in slowly decomposing litter. The overall effect of this slower N release in N rich environments may be to slow feedbacks that would otherwise lead to a “runaway N cycle”, as speculated for upland Douglas-fir forests (Perakis et al. 2006).

The stark differences in decomposition rates and patterns between red alder and Douglas-fir suggests that nutritional subsidies from red alder litter enter riparian food webs much more rapidly and in greater quantity than do subsidies from Douglas-fir litter. In addition to rapid mass loss, red alder leaves release available N to the

environment from the onset of decomposition, while Douglas-fir litter sources continue immobilizing N even after two years.

This information supports the idea that maintenance of red alder in riparian forest habitats may be desirable to sustain energy, carbon, and nutrient cycling that otherwise could limit food resource availability to consumer organisms. Collectively, this work suggests that decomposing red alder releases carbon, energy, and N more rapidly into food chains than does decomposing Douglas-fir.

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CHAPTER THREE - BIOGEOCHEMICAL CONTROLS OF DOUGLAS-FIR LITTER DECOMPOSITION

Introduction

Nitrogen (N) that is present internally in plant tissues and externally in the decomposition environment is an important regulator of litter decomposition rates (Knorr et al. 2005). The influence of N on litter decomposition is thought to be related to microbial physiology and N requirements for detrital metabolism. Fungal and bacterial microbial cells possess lower C:N (~ 5-15) than fresh leaf litter senesced from most tree species (~30-100). This disparity in C:N necessitates additional N to meet microbial metabolic demands for balanced growth when decomposing leaf litter after accounting for C losses due to microbial respiration. As a result, leaf litter with higher internal N content (lower C:N), or environments with higher ambient N supply, can both contribute to accelerated rates of leaf litter decomposition in forests.

Variation in other litter quality factors, both independently and in concert with variation in internal N, can also strongly influence litter decomposition rates. The lignin and cellulose contents are perhaps foremost among these other chemical predictors of decomposition rates for tree species litter, largely because they account for a large proportion of total litter mass, but also because they represent recalcitrant (lignin) and moderately decomposable (cellulose) chemical fractions that have widely differing decomposition dynamics (Carreiro et al. 2000). Waksman and Tenney (1927) observed that fibrous material including cellulose and lignin decomposed slower than simpler carbohydrates in agricultural residues. Subsequently, Aber and

Melillo (1982) demonstrated that the lignin:N ratio can predict decomposition rates across several temperate tree species, with higher ratios associated with slower decomposition. Since then, indices of litter quality that include information on the relative amounts of lignin, cellulose, and nitrogen – and in particular the lignin:N ratio - have proven useful for predicting litter decomposition rates in a wide range of studies worldwide (Berg and McClaugherty 2003).

Progress towards developing general predictive models of litter decomposition have most often relied on data that compare the decomposition of different species (Hobbie et al. 2006, Edmonds 1987, Melillo et al. 1989, Aber et al. 1990, Valachovic 1998). As a result, it has proven difficult to separate the roles of leaf chemistry from other leaf attributes (i.e., plant structural and morphological attributes) as factors influencing litter decomposition. The few studies that have examined the influence of initial litter quality variation within a species on decomposition rates have reported mixed results (Berg et al. 1987, Prescott 1985), thus failing to support the idea that chemical quality drives decomposition rates independent of species identity.

Douglas-fir forests of the Oregon Coast Range show high plasticity in internal N content that reflects underlying variations in soil N supply (Perakis et al. 2006), and gives rise to wide variation in litter N content within a single species. This provides an opportunity to evaluate how internal N variation of leaf litter shapes decomposition within a single species. Furthermore, site-to-site variation in N status is driven by the presence of N-fixing red alder (both in terms of red alder legacy effect and the presence or absence of alder at a particular site) and by direct N fertilization. This

provides additional opportunities to evaluate how external variation in N supply interacts with internal N concentrations to shape litter decomposition patterns.

To examine how internal (i.e., tissue) and external (i.e., site) variation in N influences decomposition of Douglas-fir (*Pseudotsuga menziesii*) litters in the Oregon Coast Range, Douglas-fir litter from eight Douglas-fir litter sources that varied widely in initial N were decomposed. I compared their responses in unfertilized and fertilized plots under Douglas-fir overstory. To further evaluate whether N fertilization resembled effects of naturally high available N, I compared decomposition in fertilized Douglas-fir plots against decomposition in naturally N-rich stands of N-fixing red alder (*Alnus rubra*). Based on the prevailing paradigm that N limits microbial growth, which in turn limits decomposition of plant material, I expected litter with higher initial N to decompose more rapidly than litter with lower initial N. I also expected that higher exogenous N availability due to N fertilization would increase decomposition rates particularly for the N-poor Douglas-fir litters. Alternatively, if N inhibits the production of the extracellular lignolytic enzymes which degrade lignin, increased N could suppress decomposition of higher N litter, particularly in site treatments with greater N availability (Carriero et al. 2000).

Methods

Study Area

The 8 study sites are located in the Alsea and Siuslaw watersheds of the Oregon Coast Range (44^{o}19'N, 123^{o}30'W) in the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1988). Major coniferous forest

species in this area include western hemlock, western red cedar (*Thuja plicata*), and Douglas-fir (Franklin and Dyrness 1988). Because large areas of these Coast Range forests are managed for commercial production of Douglas-fir, stands in this zone are often dominated by sub-climax Douglas-fir forests. Red alder dominates most of the riparian broadleaf stands, but bigleaf maple (*Acer macrophyllum*) is also found throughout Coast Range riparian forests (Pabst and Spies 1999, Nierenberg and Hibbs 2000).

Moderated by its proximity to the Pacific Ocean, maritime climate of the Oregon Coast Range is characterized by cool, wet winters and warm, dry summers. Mean annual temperature averages 10^{o}C. Annual precipitation averages 180 cm and ranges from 150 to 300 cm. Precipitation occurs primarily as rain, falling from October to April. Bedrock is composed primarily of marine derived sandstone and basaltic volcanic rock and is moderately acidic (Orr et al. 1992). Coast Range Inceptisol and Andisol soils (2004 NRCS survey) are composed of clay and sandy loams and are moderately deep with dark surface horizons high in organic matter (Franklin and Dyrness 1988).

Sites chosen for decomposition experiments were selected from a previous study of stable isotope patterns in red alder and Douglas-fir riparian forests (Scott et al. 2008) in the central and southern Coast Range (Figure 3.1 and Table 3.1). All sites are located between 15 and 75 km from the Pacific Ocean and 80 km north to south. Sites were riparian forests dominated by either Douglas-fir or red alder overstory along unconstrained reaches of 2nd to 4th order streams. At Douglas-fir dominated

sites, tree age ranged from 40-100 years. Western redcedar and western hemlock were also present, with red alder found immediately along stream banks, but not upslope of any Douglas-fir site. At red alder dominated riparian forests, trees ranged from 30-60 years in age. Bigleaf maple and conifers including Douglas-fir, western red cedar, and western hemlock were also present at red alder sites.

Of the eight riparian forest study sites I selected for decomposition experiments, four sites had overstories dominated by a mature red alder stand and four by a Douglas-fir dominated overstory (see Scott et al. 2008). At each red alder site, three 5x5m plots were randomly located within 50 m of the stream. At each Douglas-fir site, six 5x5 meter plots were randomly located within 50 m of the stream, three of which were fertilized monthly for two years with nitrogen in quantities similar to that fixed by red alder (total 150 kg N ha^{-1} y^{-1}, with half as ammonium nitrate and half as urea) (Binkley et al. 1994). The fertilized plots were located randomly among unfertilized plots, but never upslope of an unfertilized plot or within 5m of an unfertilized plot.

To support assumptions about site nutrient availability, I examined site characteristics and present the results in this section as reference material. In the autumn of 2004, 9 months after plot establishment and the initiation of fertilization, I sampled litterfall, forest floor, and surface mineral soil (0-10 cm) to evaluate potential differences in N availability and other soil characteristics between unfertilized and fertilized plots under Douglas-fir overstory and in plots under red alder overstory (Table 3.2). Litterfall N concentrations in Douglas-fir needles were nearly twice as

high in red alder as in unfertilized Douglas-fir dominated sites (sampled > 20 m away from N fertilized plots), contributing to significantly lower C:N ratios under red alder in soil and forest floor. Forest floor %N was significantly higher in red alder sites, but did not differ between unfertilized versus fertilized Douglas-fir plots. Red alder mineral soil had significantly lower C:N than either unfertilized or fertilized Douglas-fir soil, but there was no difference in soil C:N between fertilized and unfertilized Douglas-fir plots. Available inorganic N (2M KCl extractable ammonium (NH_4^+) plus nitrate(NO_3^-)) in forest floor was highest in fertilized Douglas-fir plots and lowest in unfertilized Douglas-fir plots. Soil %NO_3^- differed among all treatments with the highest in red alder soils and lowest in unfertilized Douglas-fir soils. Laboratory potential rates of N mineralization (28 day incubation at 25 °C and 75% field moisture for forest floor, and 60% water holding capacity for mineral soil) were significantly higher in red alder sites relative to either Douglas-fir treatment. Collectively, this data confirms a general pattern of higher N availability in both N fertilized Douglas-fir plots and in red alder dominated sites when compared to unfertilized Douglas-fir dominated plots. These differences permit evaluating how increases in ambient N availability in both the short-term (N fertilized Douglas-fir plots) and the long-term (red alder plots) affect Douglas-fir and red alder decomposition.

Litter Sources for Decomposition Studies

Eight sources of Douglas-fir leaf litter were collected from eight 20-30 year old stands in the Coast Range. These source stands represented the range of N

concentrations found in Douglas-fir foliage across the Coast Range, reflecting natural variation due to soil N fertility gradients (Perakis et al. 2006). At each Douglas-fir source location, I collected fresh leaf needle litter in September and October of 2003, at the time of peak needle abscission by shaking trees above exposed tarps. Fresh litter was air dried and held in paper bags in the laboratory for less than one month at room temperature during the construction of litter decomposition bags.

Decomposition of Douglas-fir leaf litter was measured using the litterbag method in which pre-weighed material is confined within mesh bags (Bobock et al. 1960). In each plot, ten bags of each of the eight Douglas-fir litter sources (see below) were placed on the forest floor. Litterbags (20 x 20 cm) were constructed using 1 mm nylon mesh upper layer and a water permeable, non-mesh nylon bottom layer to better contain Douglas fir needles. Approximately 5 grams of litter were placed in each bag. While filling litterbags, sub-samples from each air dried litter source were weighed, dried at 65° C for 48 hours, and then reweighed to determine moisture content of litter when it was deployed to the field. The moisture (in terms of mass) of litter was then subtracted from air dried mass for later calculation of decomposition rates. When bags were deployed to the field, one bag per plot was designated as collection interval zero. This bag was placed in the field along with other bags, then immediately collected into in a plastic bag and returned to the laboratory, oven dried at 65°C for 48 hours, and reweighed for mass loss during transport. This step was taken because of the tendency for dry Douglas-fir needles to work their way out of the litterbag during initial field deployment.

One bag from each litter source was collected and measured at each of eight time intervals over a two year period; 2 weeks, 1 month, 2 months, 4 months, 8 months, 1 year, 1.5 years and 2 years. At each collection, individual litterbags were cleaned off by removing freshly fallen materials and moss growth, then placed in an individual paper bag to avoid any loss of material during transport back to the lab. At the lab, the bags were oven dried at 65° C then reweighed. Lignin, cellulose, and acid-digestible fiber (ADF) were determined on initial litter samples using proximate analysis methods (Goering and van Soest 1970) at the University of Alaska Soil Laboratory. It should be noted, that when using this method, the value for acid-digestible fiber includes cellulose. Initial litter Ca, P, Mg, and K contents were determined at the Oregon State University Soils Central Analytical Laboratory. Total percent nitrogen and carbon were determined on both initial litter and remaining litter after each collection using a Costech Elemental Combustion System 4010.

Calculating Litter Decomposition Rates

Decomposition rates were calculated using a single exponential model (Valachovic et al. 2004, Harmon et al. 1990, Edmonds 1979 and 1980, Fogel and Cromack 1977) applied over the two year collection period. This exponential decomposition model has been used extensively to describe the decomposition of litter in litterbags, and produces a decomposition constant, k (y^{-1}), that serves as an integrated measure of the rate of decomposition over the time period it is calculated (Olsen 1963):

$$W_t = W_i e^{-kt} \qquad \text{(Equation 1)}$$

where W_i is the initial weight of the litter, W_t is the weight of the litter at time t, and *k* is the decomposition constant. To calculate *k*, I averaged the ratio of the mass at time of collection to the initial mass for the 3 plots at each red alder site. At each Douglas-fir sites, I averaged mass loss from the three unfertilized Douglas-fir plots and the three fertilized Douglas-fir plots. The average ratio for each source by site treatment was then log transformed and the slope of the regression line for mass versus time is defined as *k*, (Olsen 1963, Wieder and Lang 1982). By forcing the intercept (to account for 100% of biomass material at onset of decomposition), I was not able to evaluate fit using R^2. I evaluated fit by comparing *k* values from the forced model and value from a model that was not forced through 1 at t=0. The difference between these values was less than 5%, providing enough certainty that the single exponential model accurately described the decomposition pattern of Douglas-fir litter. In the literature, *k* values have been presented both forced and unforced. Following Weider and Lang (1982), I present data generated from the forced intercept model. I also evaluated the data by calculating decomposition constants using the unforced intercept model, and found the overall trends to be consistent using either method, even though the *k* values are slightly different. I therefore only show results using the forced intercept model.

N Dynamics

I examined litter N dynamics as changes in both the percent of N (relative to 100% at the onset of the experiment) and the mass of N (milligrams of N immobilized per gram of initial litter for each litter source) at each collection interval. Temporal changes in

the percent of initial N remaining provide information on relative trends in N immobilization and mineralization, but the calculated percentages over time are highly sensitive to variations in initial N content among litters. In contrast, changes in milligrams of N immobilized per gram of initial litter provide information on absolute quantities of N immobilized by different source litters.

Statistical Analyses

This experiment was designed examine how decomposition dynamics of Douglas-fir needle litter respond to variations in litter source (variations in initial litter quality of 8 Douglas-fir needle litter sources) and overstory dominance (litter decomposing in plots under red alder overstory, in unfertilized plots under Douglas-fir overstory, and in fertilized Douglas-fir plots under Douglas-fir overstory). Both the litter sources and site treatments varied in N availability, allowing me to examine the effects of both internal N (among various source litters) and external N (N availability in decomposition environment) on decomposition. N fertilization plots were included only under Douglas-fir overstory sites and not under red alder overstory, creating an unbalanced experimental design that required statistical comparisons to be made using three separate models. I applied a randomized block, split-plot design to compare decomposition in unfertilized and fertilized plots at sites under Douglas-fir overstories and evaluate potential interactions between litter decomposition rates and N fertilization. Similarly, by applying a completely randomized block design to comparisons of decomposing litter at sites under red alder and Douglas-fir overstory

(both for fertilized and unfertilized Douglas-fir), I was also able to examine potential interactions between source litter and decomposition site and examine whether artificially high N (via fertilization) affects decomposition in the same way naturally high N availability does. Details of these three models are provided below.

Model 1: Comparisons of unfertilized to fertilized Douglas-fir overstory were made using a randomized block, split-plot design. This model was used to examine the affect of N fertilization of the Douglas-fir forest floor on the decomposition of Douglas-fir litter.

1) Unfertilized vs. Fertilized plots under Douglas-fir Overstory

$Y_{jkl} = \mu + B_i + Fert_k + \gamma_{j(k)} + Source_l + Fert*Source_{kl} + \varepsilon_{ikl}$

μ	is the overall mean value of Y
Y_{ijl}	is the mean value of given response variable
B_i	is the effect of block or site, j = 1, 2, 3, 4
$Fert_k$	is the effect of fertilization (i=2), k = 1, 2
$Source_l$	is the effect of the lth litter source, l=1, 2, 3, 4, 5, 6, 7, 8
$(Fert*Source)_{kl}$	is the interaction of fertilization and litter source.
$\gamma_{j(k)}$	is the error associated with fertilization unit, which adds variability to the value of Y, $\gamma j(i_j \sim N(0,\sigma^2_a)$.
ε_{jkl}	is the random error term that adds variability to the value of Y; $\varepsilon_{jk} \sim N(0,\sigma^2)$.

Model 2: To investigate whether any differences in overstory might be due to available N, such as those under N-fixing red alder overstories, I fertilized three plots under Douglas-fir and compared the decomposition rates from fertilized plots under Douglas-fir to unfertilized plots location under red alder overstory. This model was used to test whether or not fertilizing Douglas-fir with N at a rate similar to red alder fixation to Douglas-fir plots would mimic differences in decomposition rates detected between plots under red alder and Douglas-fir overstories, i.e. decomposition rates

similar in fertilized plots at Douglas-fir sites versus naturally N rich plots at red alder sites. Unlike model 1, comparisons of Douglas-fir litter decomposition in red alder and fertilized Douglas-fir plots were made using a completely randomized design.

2) Red Alder Overstory vs. Fertilized Douglas-fir Treatment

$Y_{ijl} = \mu + Fert_i + \gamma_{j(i)} + Source_l + (Fert*Source)_{il} + \varepsilon_{ijl}$

μ	is the overall mean value of Y
Y_{ijl}	is the mean value of given response variable
$Fert_i$	is the effect of the fertilization treatment, i = 1, 2
$Source_l$	is the effect of the lth litter source, l=1, 2, 3, 4, 5, 6, 7, 8
$(Fert*Source)_{il}$	is the interaction between fertilization and source litter.
$\gamma_{j(i)}$	is the error associated with fertilization treatment, that adds variability to the value of Y, $\gamma_{j(i)} \sim N(0,\sigma^2_a)$ This represents the replication within fert*source.
ε_{ijl}	is the random error term that adds variability to the value of Y; $\varepsilon_{hij} \sim N(0,\sigma^2)$.

Model 3:. To examine the influence of overstory dominance on leaf litter decomposition rates, comparisons of Douglas-fir litter decomposition at red alder plots and unfertilized plots under Douglas-fir overstories were made using a completely randomized design.

3) Red alder vs. Douglas-fir Overstories

$Y_{ijl} = \mu + Site_i + \gamma_{j(i)} + Source_l + (Site*Source)_{il} + \varepsilon_{ijl}$

Y_{ijl}	is the mean value of given response variable
μ	is the overall mean value of Y
$Site_i$	is the effect of the site, i = 1, 2
$Source_l$	is the effect of the lth litter source, l=1, 2, 3, 4, 5, 6, 7, 8
$(Site*Source)_{il}$	is the interaction of site and litter source.
$\gamma_{j(i)}$	is the error associated with site, that adds variability to the value of Y, $\gamma_{j(i)} \sim N(0,\sigma^2_a)$ This represents the replication within site*source.
ε_{ijl}	is the random error term that adds variability to the value of Y; $\varepsilon_{hij} \sim N(0,\sigma^2)$.

Statistical analysis was performed using SAS v 9.1 statistical software (SAS Institute Inc 2003). Proc MIXED was used to generate *k* from the single exponential model. Analysis of variance (ANOVA) F-tests were used to test for effects of source, stand, and fertilization treatments in the framework of models 1, 2, and 3. These tests are modifications of models 1, 2, and 3. Source litter is not included, but variation assignments for site treatment and fertilization are the same. Normal probability plots were examined to evaluate data distribution assumptions. Correlations among initial litter chemical variations were evaluated using Pearson Correlation Coefficients table for initial litter chemical factors. Significance levels were set at $p<0.05$ prior to analysis.

I used 2 methods to examine how the initial litter quality of the eight Douglas-fir litters influenced decomposition. Within a common overstory (red alder or Douglas-fir) and fertilization treatment (fertilized plots under Douglas-fir overstory), I employed Akaike Information Criterion (AIC) to examine which initial chemical factor(s) had the best predictive power. For this evaluation, the model that reported the smallest AIC value is preferred. I examined the AIC (Akaike Information Criterion) values from regression analyses of the 11 initial chemical factors measured in this study, as well as a completely random model which served as the null model against which the other AIC values were compared. The resulting AIC values were ordered from smallest to largest. Similar to other studies employing AIC to rank the strength of different models, I chose a value of 4 AIC units to indicate competing

models, i.e., any value within 4 AIC units of the smallest value suggests that those factors predict decomposition rates equally well. While AIC is useful for examining the influence of initial litter quality factors on decomposition within a given fertilization or overstory treatment, to examine both the relationship between initial litter quality factors and decomposition rates of the eight Douglas-fir litter, as well as how the fertilization or overstory treatments may influence the nature of these relationships, I employed a hierarchical linear model (HLM). The HLM model incorporates data from multiple levels (source and site treatment) to determine the impact of both individual and grouping factors upon some individual level outcome.

Results

Initial Litter Chemistry

I evaluated several measures of initial litter quality, including nutrient concentrations (N, Ca, K, Mg, P), carbon fractions (total carbon, acid digestible fiber, cellulose, lignin) and integrated litter quality measures such as C:N, lignin:N, and the lignocellulose index (LCI = lignin / (lignin + cellulose)) (Table 3.3). Overall, variations in nutrient concentrations among source litters were substantial in comparison to carbon fraction variations, consistent with expectations of a single species' litter collected from sites that vary widely in soil nutrient availability. Initial N in the eight litter sources ranged 2-fold, from 0.62 to 1.26%. Initial nutrient concentrations also varied for P (0.07 - 0.11%), Ca (0.7 – 1.4%), Mg (0.08 – 0.13%), and K (0.15 – 2.5%). Litter lignin ranged from 29 – 35%, cellulose ranged from 13 – 21%, acid digestible fiber ranged from 49 to 56%, and LCI ranged from 0.60 to 0.73.

Variations observed in litter C:N (range: 41 to 76) and lignin:N (range: 27 to 52) were mostly due to variations in %N.

Several litter chemical components from the eight Douglas-fir source litters were correlated with one another (Table 3.4). Among the nutrients, I found that N, Ca, and Mg were correlated with one another, and P was correlated with K. The lignin:N ratio was correlated significantly with N but not lignin. Likewise, the C:N ratio was correlated significantly with both C and N, although N explained a larger proportion of this variation. Litter N was also correlated positively with cellulose.

Leaf Litter Decomposition

Both mass loss and decomposition rates of the eight Douglas-fir litter sources indicate that litter quality plays an important role in decomposition (Table 3.5, 3.6 and Figures 3.2, 3.3). After two years, the percent biomass remaining of the eight Douglas-fir litter sources ranged from 53 to 63% in unfertilized plots under Douglas-fir overstory, 65 to 69% in fertilized plots under Douglas-fir overstory, and 56 to 69% under red alder overstory (Table 3.6). Surprisingly, litter with lower initial N lost more mass after 2 years than litter with higher initial N. In addition, each source of litter lost less mass under fertilized than unfertilized Douglas-fir plots (Table 3.6).

Results from ANOVA comparing decomposition rates paralleled those of mass loss. Douglas-fir decomposition rates ranged from 0.22 – 0.30 y^{-1} in unfertilized plots and from 0.18 – 0.23 y^{-1} in fertilized plots under Douglas-fir overstory (Table 3.6 and Figure 3.2). Decomposition rates ranged from 0.18 – 0.27 y^{-1} under red alder sites. Similar to the trends observed for mass remaining at 2 years, litter with lower initial N

decomposed more rapidly than higher initial N litter. Examinations of relationships between the litter quality measures and decomposition rate are explored below.

Litter Quality Effects

To evaluate which of the initial litter chemical factors had the most predictive power under a particular overstory or fertilization treatment (unfertilized or fertilized plots under Douglas-fir and under red alder), I ran a regression of decomposition rate versus any one initial litter constituent evaluated in this experiment (Ca, K, Mg, N, P, ADF, cellulose, lignin, lignin:N, and LCI). Results from the AIC analysis suggest that the relationship between decomposition and initial litter quality depends on the environment of decomposition (Table 3.7). In unfertilized plots under Douglas-fir, AIC rankings showed that all the initial nutrients measured, as well as ADF, cellulose, and lignin:N were correlated with decomposition (i.e., these models all ranked within 4 AIC units of the smallest value, indicating they can all reasonably predict decomposition rates). In fertilized plots under Douglas-fir, measures of carbon quality (LCI and cellulose), and the lignin:N ratio had the smallest AIC values within 4 units of small values. In red alder plots, nutrients Ca and N and the lignin:N ratio were within 4 AIC units of the smallest value and thus are likely to have the greatest influence on decomposition.

Hierarchical Linear Model

Because AIC analysis is unable to examine both the relationship between initial litter quality factors and decomposition rates of the eight Douglas-fir litters, and how the fertilization or overstory treatments may influence the nature of these relationships, I employed a hierarchical linear model (HLM) (Tables 3.8a and 3.8b, Figures 3.4-3.13). As suggested by the biomass loss and decomposition rate trends, initial litter N was negatively correlated with decomposition rate (Table 3.8a, Figure 3.4). Decomposition rates in both unfertilized plots under Douglas-fir overstories and those under red alder overstories were higher than rates from fertilized plots under Douglas-fir (Table 3.8a, Figure 3.3). Comparisons of fertilized Douglas-fir vs. red alder sites indicate that artificially adding N to plots at Douglas-fir sites does not increase rates of decomposition to match those in naturally N-rich red alder sites. In fact, rates under fertilized conditions were reduced.

Across all statistical models, initial litter Ca was positively correlated to decomposition for the eight Douglas-fir litter sources (Table 3.8a, Figure 3.5), but this relationship was not influenced by fertilization or overstory. For comparisons of unfertilized versus fertilized plots under Douglas-fir overstories, Mg was negatively correlated and P was positively correlated with decomposition (Table 3.8a, Figures 3.6 and 3.7). HLM indicated that neither Mg or P were significantly related to decomposition when comparing fertilized Douglas-fir plots with plots under red alder or overstory (fertilized Douglas-fir versus red alder). Since both Mg and P were correlated under other model comparisons, it is likely that this lack of correlation was

due to added variation between overstories that did not occur in the blocked design comparing unfertilized and fertilized plots under Douglas-fir. Decay rate (*k)* was not related to decomposition rate under any of the three model frameworks (Table 3.8a, Figure 3.8). Cellulose, lignin:N and LCI were related to decomposition for comparisons of unfertilized versus fertilized plots under Douglas-fir (Table 3.8b, Figures 3.10, 3.12, 3.13). Across all treatments, cellulose was negatively correlated with decomposition among the eight source litters, while both lignin:N and LCI were positively correlated with decomposition.

Litter N Dynamics

The initial percent N Douglas-fir litter sources ranged from 0.68 – 1.22% (6.8 - 12.2 mg N/g litter) (Table 3.9). While some aspects of N dynamics differed among source and overstory and fertilization treatments, general trends indicate that all Douglas-fir litter sources immobilized N over much of the experiment. Depending on overstory and fertilization treatment, only zero to three of the eight Douglas-fir litter sources (generally those with high initial N) began mineralizing N towards the end of the 2 year period.

In unfertilized plots under Douglas-fir, the percent of original N remaining over time displayed some seasonal oscillation between immobilization and mineralization, although N was immobilized overall during the 2 year period. In unfertilized plots under Douglas-fir, DF1 (the most N-poor litter) immobilized 151% of initial N and was trending towards more immobilization. In contrast, DF8 (the

most N-rich litter) had begun mineralizing N by the end of the 2 year period and was at 83% of initial N at the end of year two (Table 3.9, Figure 3.14). In fertilized Douglas-fir plots, all litter sources decomposing in fertilized Douglas-fir plots immobilized N (Table 3.9, Figure 3.14). Under red alder overstories, half of the litter sources were continuing to immobilize N after 2 years, while the other 4 sources of Douglas-fir litter had begun to mineralize N (Table 3.9, Figure 3.14).

While examining the percent of initial N can illustrate overall trends in immobilization and mineralization, it doesn't provide a measure of how much N is gained or lost during decomposition. Examinations of the amount of N (mg) immobilized per gram of initial litter indicate that overall patterns paralleled those of the percent of initial N. After two years of decomposition, the milligrams of N immobilized per gram of initial litter ranged from 15.9 - 19.6 mg N/g in unfertilized plots under Douglas-fir, from 16.9 – 22.4 mg N/g in fertilized plots under Douglas-fir, and from 17.0 - 21.7 mg N/g under red alder (Table 3.9). In all decomposition sites (unfertilized and fertilized Douglas-fir, and red alder overstories), litter with low initial N immobilized the greatest quantity of N after 2 years. In unfertilized Douglas-fir plots, low N (DF1) litter immobilized the most mg N per gram of initial litter (3.43) after 2 years, and only DF5, DF7 and DF8 began mineralizing N (0.64, 0.93 and 2.24 mg N per gram of initial litter respectively) (Table 3.9, Figure 3.15). In fertilized plots under Douglas-fir, all eight litter sources immobilized N over the 2 year period. Under red alder, only DF7 and DF8 starting to mineralize N within two years (Table 3.9).

I employed a hierarchical linear model to examine the relationship between initial N and the amount of N (mg) immobilized per gram of initial litter and whether this relationship differs depending on the overstory or fertilization treatment. Results indicate a negative correlation between the amounts of N (mg) immobilized per gram of initial litter and its initial percent N. That is, litter with lower initial N immobilized more N per gram of initial litter than litter with higher initial N. While results from the HLM do not suggest significant differences in N immobilized depending on overstory or site treatment, both red alder and fertilized Douglas-fir treatments tended to immobilize more N than unfertilized plots,.

In general, the C:N of different source litters converged during the decomposition process. At the onset of the experiment, initial litter C:N ranged from 41 (DF8) to 76 (DF1). After 2 years, the range of C:N of Douglas-fir litter sources had narrowed to 22 to 31 at red alder sites, 28 to 32 at unfertilized plots and 23 to 30 at fertilized plots at Douglas-fir sites (Table 3.9 and Figure 3.17).

Discussion

Average Douglas-fir litter decomposition rates over the two year experiment ranged from 0.18 to 0.30 y^{-1} across all eight Douglas-fir litter sources and site treatments. Of the many studies that have examined Douglas-fir litter decomposition, only a few calculated decomposition rates over a comparable 2 year period. Of these, Fogel and Cromack (1977) reported decomposition rates ranging from 0.22 to 0.38 y^{-1} and rates reported by Edmonds (1979 and 1980) ranged between 0.40 to 0.56 y^{-1}. Edmonds (1980) suggested that the more rapid rates of decomposition he observed

could be attributed to increased summer rains in Washington. Other studies report decomposition constants for Douglas-fir litter ranging from 0.22 to 0.56 (Harmon et al. 1990, Valachovic 1998) but these values were calculated over a one year period and are not directly comparable to the *k* values presented in this study because decomposition rates in this study were calculated over a 2 year period.

Overall, results from the hierarchical linear model indicate that both internal N (initial differences among eight litter sources) and external N (N fertilization of Douglas-fir) were correlated negatively with decomposition rates. Other litter quality variables were also correlated with decomposition but the suppressed decomposition I observed in N fertilized Douglas-fir plots provides experimental evidence that N directly regulates decomposition of Douglas-fir litter.

Litter Quality Relationships to Decomposition

Several litter carbon fractions and nutrient constituents measured in my study were interrelated (Table 3.4), so it is not surprising that multiple factors were significant predictors of decomposition variations observed among the eight sources of Douglas-fir litter (Table 3.7). As a result, additional information must be used to discern which variable(s) are most likely to be influencing decomposition. Lignin:N was the only factor which occurred as a competing AIC model for predicting decomposition in all incubation environments and across all HLM comparisons, and was positively related to decomposition (Table 3.7). This is opposite the pattern typically reported worldwide, where lignin:N correlates negatively with decomposition (e.g. Mellilo et al. 1982, Harmon et al. 1990). When interpreting the

results found here, it is important to recognize that variation in lignin:N among Douglas-fir litters arose primarily from variation in N content, not lignin (Table 3.4). This explains why N was also among the competing AIC models for predicting decomposition, whereas lignin was not, and indicates that the ability of lignin:N to predict decomposition in this study is attributable primarily to variations in litter N content. Indeed, my results suggest that litter N is *negatively* related to decomposition rate.

Overall, the litter carbon fractions that I measured (i.e., lignin, cellulose, LCI, ADF) did not vary greatly among the eight different source litters, yet several of these measures emerged as significant predictors of Douglas-fir decomposition (Table 3.7). Generally, however, these correlations are atypical and difficult to explain based on previous work. For example, I found a positive association between LCI and decomposition rate, but increasing LCI signals an increasing proportion of decomposition-resistant lignin fractions, which should contribute to slower decomposition overall, particularly for lignin occurring in N-rich litter (Berg et al. 1987). An evaluation of sixteen shrub and tree species across the Pacific Northwest (including Douglas-fir) found that both lignin and LCI correlate negatively with decomposition rate, as expected (Valachovic et al. 2005). The lignin content of the Douglas-fir litters examined here averaged 32% (range: 29-35%), above the 30% value where lignin fails to effectively predict decomposition (Knorr et al. 2005). Overall, it seems unlikely that the variations in proximate chemical factors observed among litters in this study are responsible for the observed decomposition differences.

Litter P and Ca concentrations also emerged as significant predictors of decomposition rate (Tables 3.7 and 3.8). The correlation of decomposition with P content of litter is not likely a causal relationship, however, since another ongoing experiment with Douglas-fir at nearby sites has found that experimentally increased litter P content does not influence decomposition rate (Tiffany van Huysen et al. pers. comm.). In the current study, Douglas-fir litter Ca concentrations were positively correlated with decomposition rates and negatively correlated with litter N concentrations, making it difficult to determine the individual role of Ca in decomposition. Other work has suggested that litter Ca content can influence decomposition rates and forest floor turnover (Hobbie et al. 2006, Reich et al. 2005), and Ca deficiency has been suggested as a possible factor limiting for forest growth and other processes in coastal Oregon forests (Perakis et al. 2006).

My results suggest that high litter N concentrations slow the decomposition of Douglas-fir litter (Table 3.7), which may be related to the high lignin content of Douglas-fir. High N content decreases lignin breakdown in conifer needles (Berg et al. 1987), and Douglas-fir has among the highest total lignin content (acid hydrolysable lignin plus acid unhydrolyzable residue) of any shrub or tree species in the Pacific Northwest (Valachovic et al. 2004). The mechanism for slower decomposition of N-rich, lignin-rich litter is not definitively known, but may be related to inhibition of microbial synthesis of ligninase enzymes, as occurs when N is added externally to high-lignin litter (Sinsabaugh et al. 2002). The slower decomposition that I found in Douglas-fir litter fertilized with N (discussed below)

indirectly supports this hypothesis. However, not all studies have found high N content inhibits conifer decomposition. For example, Berg et al. (1982) found that differences in N content of Scots Pine needles did not affect overall litter decomposition rates over three years, and Prescott (1995) reported no difference in jack pine litter decomposition over three years despite a five fold difference in N content. While it is difficult to generalize from these few studies, the range of results suggest that the lignin:N ratio is not universally applicable for predicting decomposition rates of forest species litter. This may complicate assessments of how added N (e.g., by fertilization or deposition) will influence ecosystem C cycles, particularly in forests dominated by long-lived conifers that can alter their foliar and litter N in response to changes in N supply.

Decomposition Site and Decomposition

I added N fertilizer to Douglas-fir plots at rates similar to biological N fixation by red alder (150 kg N ha^{-1} y^{-1}), and therefore expected similar changes in decomposition rates in these two treatments relative to unfertilized Douglas-fir plots. However, my results indicated that while external N fertilization decreased needle decomposition rates in Douglas-fir sites, no significant changes in decomposition rate occurred when needles were decomposed under red alder. Although the reason for differences between red alder and fertilized Douglas-fir plots remains unclear, my results provide direct support for the idea that externally added N slows Douglas-fir needle decomposition. Considering the high average lignin content (~ 32%) of the Douglas-fir needles studied here, these findings are broadly consistent with results

from a recent meta-analysis showing slower decomposition of lignin-rich litter (> 30% lignin) when N was added externally (Knorr et al. 2005).

Fog (1988) outlined four possible explanations that could lead to suppression of decomposition rates of litter with high lignin decomposing in N rich environments. The first hypothesis suggests that elevated N can increase competition between microorganisms and can alter the outcome of competition between different types of decomposers. A second hypothesis suggests that amino compounds condense with polyphenols and other decomposition products forming byproducts that are extremely resistant to decomposition and break down very slowly. Another hypothesis suggests that excess N reduces the efficiency of extra-cellular enzyme by contributing to the randomization of chemical bond structures of organic materials. The last hypothesis suggests that the extra-cellular production of ligninase enzymes (which degrade lignin) by white-rot fungi is suppressed in the presence of high N availability. Specifically, ligninase is produced only when the fungi have switched from primary to secondary metabolism, which is not driven by the presence of degradable lignin, but instead is triggered by the exhaustion of available N (Keyser et al. 1978). Similarly, Carreiro et al. (2000) found that added N stimulated cellulose activity (e.g., labile dogwood decomposed more quickly in response to N additions), but inhibited phenol oxidase activity (e.g., lignified oak leaves decompose more slowly in response to N addition). There is growing support for the idea that the decomposition of lignin (and other carbon-containing molecules) is influenced by the response of microbial communities and specific extracellular enzymes to added N (Sinsabaugh et al. 2002).

The high lignin content of Douglas-fir needles examined in this study may therefore be above a threshold (Knorr et al. 2005) where added N slows lignin decomposition more than it accelerates the decomposition of labile carbon compounds.

It remains unclear why external N fertilization slowed needle decomposition in Douglas-fir plots, but red alder sites with naturally high N availability did not show this pattern. Both N fertilized sites and red alder sites displayed high ambient N availability (Table 3.2), but it is possible that direct N fertilization had stronger effects on those specific properties that most strongly influence litter decomposition. It is also possible in red alder sites that the inhibitory effect of high external N was offset by other factors that promote decomposition, such as more favorable microclimate or decomposer communities. Regardless of the mechanism, this is the first study demonstrating that N fertilization slows the decomposition of Douglas-fir needles under field conditions, and complements previous work showing that N fertilization suppresses soil organic matter respiration in Douglas-fir forests (Swanston et al. 2004). N fertilization thus appears to slow organic matter turnover along the decomposition continuum from needle to humus in Douglas-fir forests, and may promote detrital and soil carbon storage in forests of this region (Adams et al. 2005).

Finally, while external N fertilization did suppress the decomposition of Douglas-fir litter overall, this effect did not depend on the initial %N of the Douglas-fir litters (Table 3.5, Figure 3.3). Thus, there do not appear to be any synergistic effects of internal and external N on Douglas-fir needle decomposition, even though each factor individually resulted in slower decomposition at higher N. I found only a

slight interaction ($p = 0.06$) between initial litter quality and site treatment for decomposition comparisons in fertilized Douglas-fir sites versus red alder sites (Table 3.5). This interaction was marked by a tendency for high-N litter to decompose similarly in both sites, but for low-N litter to decompose more rapidly under red alder (Figure 3.3). Because the presence of N-fixing red alder can greatly increase litter N concentrations in co-occurring Douglas-fir (Table 3.2, and Binkley et al. 1992), which results in slower Douglas-fir litter decomposition (Table 3.7), it seems possible that mixed stands of these species could result in slower Douglas-fir litter decomposition than occurs in pure Douglas-fir stands. While this idea has not been tested directly, decomposition rates of red alder and Douglas-fir litter mixtures do not differ from the decomposition of the individual litters alone (Prescott et al. 2005).

Litter N Dynamics

The rate and nature of N cycling are closely tied to the decomposition of leaf litter (Prescott 2005). The percent of N often increases in remaining plant material as decomposition progresses. This increase in N is especially common in species with low initial N concentration and presumably results from accumulations by decomposing microbes (Fahey 1983, Parton et al. 2007). The assumption is that early in decomposition when relatively easily digestible carbon is readily available, microbes are limited by low nutrient concentrations and must draw them in from the environment to continue consuming carbon. My results show that litter N concentrations increased for all 8 litter sources during decomposition across all site treatments, with the quantity of N immobilized correlated negatively to initial litter N

concentration (i.e. low-N litter immobilizes more N than high-N litter) (Table 3.9, Figure 3.16). By conventional thinking, this suggests that microbes decomposing the lower N litter are limited by low levels on N in the litter. However, since higher-N litter decomposes more slowly than lower-N litter, and decomposition is suppressed under conditions of elevated N, it is difficult to understand why this N was immobilized, and what role immobilized N plays in overall decomposition rates. It is possible that microbes present on the litter, other than white-rot fungi that specialize in degrading lignin, are drawing in N to decompose other molecules in the litter. It is also possible that this N was immobilized by ion exchange processes occurring on charged surfaces created during litter decomposition, or by microorganisms that colonized the litter but otherwise were not involved directly in litter decomposition.

N dynamics during decomposition have been linked to several aspects of initial litter chemistry including N (Melillo et al 1982), lignin:N (Scott and Binkley 1997, Mellilo et al. 1982) and C:N (Agren and Bosatta 1996, Chapin 2003). In this study, differences in litter quality that influenced litter N dynamics were most likely driven by differences in initial N, since differences in lignin and C varied little compared to the wide variation in initial N. Net N mineralization vs. immobilization during the decomposition process is often related to a "critical" C:N ratio in decomposing litter (Berg and Staaf 1981, Aber and Melillo 1982, Edmonds 1979 and 1980, Prescott 2005). This critical value varies between ecosystems and plant species, but Berg and Staaf (1981) suggest this ratio is related to decomposition rate. Edmonds (1979, 1980) reported critical ratios for forest litters in the Pacific Northwest from 23 to 35. In this

study, litter C:N across all sources under all site treatments ranged between 22-32 after 2 years (starting with a C:N range from 41-76), with most litter sources immobilizing N over that full period, and just a few litter sources demonstrating initial phases of N mineralization towards the end of 2 years (Figure 3.14). However, I found that among-litter variation in immobilization / mineralization was not clearly related to C:N, perhaps because all litters were relatively close to the critical ratio.

Ambient nitrogen in the decomposition environment can also influence litter N dynamics. Several studies have shown greater immobilization of N into litter that decomposes in forest floors that are naturally N-rich or artificially fertilized (Hirschfield et al. 1984, O'Connell 1986, Pastor et al. 1987). The observation here of increased N immobilization under red alder and in fertilized plots under Douglas-fir (Table 3.9 and Figures 3.15 and 3.16) suggests that high N availability in the decomposition environment can delay net mineralization, potentially driven by luxury uptake of N, since N is not limiting to decomposition overall. In fact, the onset of net N mineralization was strongest in unfertilized Douglas-fir plots, despite their having the lowest available N of the sites studied. This is consistent with Thomas and Prescott (2000) who found even though Douglas-fir has low N litter concentrations relative to other western conifers, Douglas-fir forest floors display the highest N concentration and N mineralization of species examined (Douglas-fir, red alder, lodgepole pine (*Pinus contorta),* and western hemlock).

N mineralization has been proposed as a primary feedback mechanism in terrestrial nutrient cycling (Ehrenfeld et al. 2005). Several studies have demonstrated

the linkage between decomposition and mineralization rates, suggesting a positive feedback mechanism whereby more rapid decomposition and more rapid N cycling occurs in sites with higher N availability (Gosz 1981) and slower rates of decomposition contribute to slower rates of nutrient mineralization and prolonged periods of immobilization (Waring and Schlesinger 1985, Gosz 1981, Edmonds et al. 1990). Ultimately, feedbacks associated with slower decomposition rates may reduce forest primary productivity through the accumulation of organic matter and immobilization of N and other nutrients in the forest floor (Berg et al. 1987). However, the patterns in decomposition and N dynamics observed in the current study are not so easily characterized by such positive feedbacks. I found that litter with lower initial N immobilized more N and decomposed more rapidly, while litter with higher initial N immobilized less N and decomposed more slowly. Furthermore, adding N to the decomposition environment suppressed decomposition rates of all litter sources, suggesting a negative feedback mechanism between decomposition and N availability, whereby supplemental N actually slows decomposition, locking up both carbon and N. The exceptionally high soil C and N accumulation observed in some Oregon Douglas-fir forests, while ultimately a legacy of high historical N inputs from N-fixing red alder (Scott et al. 2008, Sinkhorn 2008), may be maintained by negative feedback from high N availability that promotes C and N stabilization in soils (Swanston et al. 2005). Given that decomposition is suppressed under conditions of elevated N availability, this further suggests a negative feedback mechanism for

carbon and nitrogen cycling in Douglas-fir stands, particularly when N availability is higher than typical ambient conditions for Douglas-fir stands.

Conclusions

Overall, this study provides insight into how initial chemical characteristics of litter quality influence the rate of decomposition within a single species. Contrary to many studies across species, N does not positively influence decomposition whether there is more N in initial litter or in the decomposition environment. The experimental finding that N addition reduced decomposition is consistent with slower decomposition of high N litter, and points to an important role for N in regulating decomposition in this study. This raises the possibility that initial N content is the most functionally important litter chemical predictor of Douglas-fir litter decomposition rates. While the suppression of ligninase enzyme is the most likely explanation, the greater immobilization of N in low N litter suggests that other mechanisms could underlie N dynamics.

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CHAPTER FOUR – OVERALL CONCLUSION

The overall objective of this thesis was to examine the decomposition dynamics of red alder and Douglas-fir leaf litter and evaluate how both species and site influence the rate and temporal pattern of decomposition in Coast Range riparian forests. Broad decomposition patterns of red alder and Douglas-fir leaf litter followed expected trends with higher quality red alder litter decomposing more rapidly than lower quality Douglas-fir litter. Red alder litter decomposed very rapidly in early stages of decomposition followed by a dramatic decrease in mass loss. Douglas-fir litter was modeled using a single exponential decomposition pattern. The rapid decomposition of red alder litter was especially pronounced in red alder sites. However, after the fast pool of red alder litter had decomposed, the remaining proportion decomposed more slowly than Douglas-fir litters. The stark differences in decomposition rates and patterns between red alder and Douglas-fir suggests that nutritional subsidies from red alder litter enter riparian food webs much more rapidly and in greater quantity than do subsidies from Douglas-fir litter. The rapid initial decomposition of red alder may be especially important in subsidizing terrestrial food webs where a substantial portion of leaf litter is transported off site and into streams, such as in steeply sloped riparian areas common to the Oregon Coast Range.

I also evaluated how initial chemical characteristics of litter quality influence the rate of decomposition within a single species, Douglas-fir. Contrary to earlier findings derived from studies across different species, I found that neither internal tissue N nor external environmental N was correlated positively with decomposition

rates in Douglas fir. In both cases, increased N was related negatively to decomposition rates. The experimental finding that N addition reduced decomposition is consistent with slower decomposition of high N litter, and points to an important role for N in regulating decomposition in this study. This raises the possibility that initial N content is the most functionally important litter chemical predictor of Douglas-fir litter decomposition rates. While the suppression of ligninase enzyme is the most likely explanation, the greater immobilization of N in low N litter suggests that other mechanisms could underlie N dynamics.

In riparian forests of the Oregon Coast Range, previous site occupancy by red alder may increase site N availability that facilitates rapid Douglas-fir growth, but such effects do not appear to increase site nutrient availability greatly though nutrient recycling and feedback mechanisms linked to litter decomposition. Reduced rates of decomposition of Douglas-fir litter in fertilized plots under Douglas-fir overstories further suggest that N may actually slow decomposition, particularly for high-N litter.

N dynamics were markedly different both when compared across species and with Douglas-fir litter sources. Red alder litter N was released from decomposing litter from the onset of decomposition indicating that there is sufficient N contained within the litter substrate to meet microbial demand. In contrast, N concentrations increased for all 8 Douglas-fir litter sources during decomposition across all site treatments; with the quantity of N immobilized correlated negatively to initial litter N concentration (i.e. low-N litter immobilizes more N than high-N litter). By conventional thinking, this suggests that microbes decomposing the lower N litter are

limited by low levels on N in the litter. However, since higher-N litter decompositions more slowly than lower-N litter, and decomposition is suppressed under conditions of elevated N, it is difficult to understand why this N was immobilized, and what role immobilized N plays in overall decomposition rates. It may be possible that this N was immobilized by ion exchange processes occurring on charged surfaces created during litter decomposition, or by microorganisms that colonized the litter but otherwise were not involved directly in litter (or at least lignin) decomposition.

Collectively, this work suggests that decomposing red alder releases carbon and N more rapidly into food chains than does Douglas-fir. This information supports the idea that maintenance of red alder in riparian forest habitats may be desirable to sustain energy, carbon, and nutrient cycling that otherwise could limit food resource availability to consumer organisms. Intuitively it makes sense to balance large wood and shade needs traditionally associated with coniferous forests with the nutritional values provided by broadleaf riparian vegetation

Table 2.1. Site, location, elevation and soil characterization of the 8 research sites (4 dominated by red alder and 4 by Douglas-fir).

Site	Riparian Overstory	Location	Elevation (m)	Soil series of stream and surrounding area	Classification
Honey Grove Creek					
	Red alder	44° 20'N, 123° 38' W	139	Elsie silt loam	Silty alluvium derived from sandstone
				Treharne-Eilertsen-Zyzzug complex	Silty alluvium derived from sandstone
Nelson Creek					
	Red alder	44° 36'N, 123° 36' W	165	Meda loam	Alluvium and colluvium derived from sandstone
				Preacher loam	Colluvium and residuum derived from sandstone
Smith Creek					
	Red alder	43° 50'N, 123° 22' W	263	Peavine silty clay loam	Colluvium and residuum derived from sandstone
				Digger-Bohannon complex	Colluvium and residuum derived from sandstone
				Bohannon gravelly loam	Colluvium derived from sandstone
Record Creek					
	Red alder	44° 20'N, 123° 38' W	137	Treharne-Eilertsen-Zyzzug complex	Silty alluvium derived from sandstone
				Meda-Treharne-Wasson complex	Loamy alluvium and colluvium derived from sandstone
					Silty alluvium derived from sandstone
Alsea River Tributary					
	Douglas-fir	44° 19'N, 123° 28' W	284	Bohannon-Preacher complex	Colluvium and residuum derived from sandstone
				Nekoma-Fluvaquents complex	Recent loamy alluvium derived from sandstone
S. Fork Alsea Tributary					
	Douglas-fir	44° 21'N, 123° 34' W	299	Honeygrove-Shivigny complex	Clayey colluvium and residuum derived from basalt
				Elsie silt loam	Silty alluvium derived from basalt
				Meda-Treharne-Wasson complex	Loamy alluvium and colluvium derived from basalt
					Silty alluvium derived from basalt
Wolf Creek					
	Douglas-fir	43° 55'N, 123° 21' W	187	Jory silty clay loam	Loamy colluvium derived from sandstone
				Eilertsen silt loam	Alluvium derived from sandstone
Yew Creek					
	Douglas-fir	44° 30'N, 123° 33' W	588	Hemcross-Klistan complex	Colluvium and residuum derived from basalt
				Meda-Treharne-Wasson complex	Loamy alluvium and colluvium derived from basalt
					Silty alluvium derived from basalt

Table 2.2. Litterfall, forest floor, and soil characteristics (n=4) for each treatment.

Site Characteristic	Unfertilized Douglas-fir	Fertilized Douglas-fir	Red alder
Litterfall			
Red alder Litterfall N (%)	2.1 ±0.03	..	2.2 ±0.03
Red alder Litterfall C (%)	52.3 ±0.28	..	52.0 ±0.06
Red alder Litterfall C:N	24.4 ±0.28	..	24.0 ±0.29
Douglas-fir Litterfall N (%)	0.8^{b} ±0.01	..	1.3^{a} ±0.14
Douglas-fir Litterfall C (%)	53.1 ±0.08	..	53.2 ±0.28
Douglas-fir Litterfall C:N	70.1^{b} ±0.76	..	43.8^{a} ±3.36
Forest Floor			
Forest Floor N (%)	1.10^{b} ±0.02	1.20^{b} ±0.06	1.66^{a} ±0.06
Forest Floor C (%)	47.92^{b} ±0.56	48.27^{b} ±0.76	41.91^{a} ±0.98
Forest Floor C:N	43.79^{b} ±1.21	41.12^{b} ±1.77	25.78^{a} ±1.35
Forest Floor $NH_4^+ + NO_3^-$ (mg/kg)	0.31^{b} ±0.06	4.14^{c} ±0.59	2.85^{a} ±0.32
Forest Floor NO_3^- (%)	7.17^{b} ±2.31	22.28^{c} ±1.50	41.56^{a} ±2.85
Forest Floor N Mineralization	0.98^{b} ±0.63	2.21^{b} ±0.45	10.28^{a} ±0.65
Forest Floor Nitrification (%)	80^{b} ±23.0	94 ±13.9	74^{a} ±2.3
Soil			
Soil N (%)	0.25 ±0.01	0.32 ±0.01	0.30 ±0.02
Soil C (%)	6.24 ±0.50	9.25 ±1.05	5.45 ±0.60
Soil C:N	24.45^{b} ±0.74	28.24^{b} ±1.99	17.92^{a} ±0.70
Soil $NH_4^+ + NO_3^-$	0.15^{a} ±0.04	0.42^{b} ±0.08	0.29^{a} ±0.03
Soil NO_3^- (%)	21.48^{b} ±1.96	51.75^{c} ±3.50	87.05^{a} ±2.07
Soil N Mineralization	0.64 ±0.21	0.58 ±0.09	0.64 ±0.06
Soil Nitrification (%)	61^{b} ±0.07	59^{ab} ±1.2	100^{a} ±na
Soil Bulk Density (g/m^3)	0.54 ±0.01	0.59 ±0.01	0.55 ±0.04
Soil pH	6.38^{b} ±0.13	5.75^{c} ±0.15	5.32^{a} ±0.14

Notes: The reported values are the mean of the 4 site or fertilization treatment replications. Different letters indicate significant statistical differences ($p<0.05$) between red alder overstory and unfertilized plots under Douglas-fir overstory ($F_{1,6}$), red alder overstory and fertilized plots under Douglas-fir overstory ($F_{1,6}$), and for comparisons between unfertilized and fertilized plots under Douglas-fir overstory ($F_{1,3}$). Standard error is from four replicates of each overstory or fertilization treatment based on 4 replications of overstory or fertilization treatment.

Table 2.3. Initial chemical composition of senesced leaf litter from red alder and from low- and high-N Douglas-fir litter sources.

	Percent of Original Litter Material											
	Nutrients					Carbon Compounds				Integrated Measures		
Source Litter	**N**	**P**	**Ca**	**Mg**	**K**	**C**	**ADF[a]**	**Cellulose**	**Lignin[b]**	**Lignin:N**	**C:N**	**LCI[c]**
Douglas-fir 1 (DF 1)	0.68	0.10	1.42	0.08	0.20	51.4	49.4	13.0	35.0	51.8	76.1	0.73
Douglas-fir 7 (DF 7)	1.21	0.09	0.70	0.12	0.20	53.7	51.5	18.4	33.0	27.2	44.2	0.65
Red alder (RA)	2.34	0.09	0.46	0.18	0.46	53.0	17.7	8.3	9.3	4.0	22.6	0.62

Note: [a] Acid-digestible Fiber (ADF) and lignin determined following Goering and van Soest (1970). Ligno-cellulose index (lignin+cellulose/lignin) calculated following Melillo et al. (1989).

Table 2.4. Data table for percent biomass remaining (%), single exponential equivalent *k* ($k_{e\ (}y^{-1}$)), single exponential decomposition of Douglas-fir $k_{s\ (}y^{-1}$), and double exponential decomposition of red alder (unconstrained slow pool ($k_s\ (y^{-1})$), fast pool (k_f, (y^{-1})), and the proportion of mass (m_f)), and constrained slow pool ($k_s\ (y^{-1})$) and fast pool (k_f, (y^{-1}))), after 2 years of decomposition. Values in parentheses represent the standard error calculated for each overstory or fertilization treatment (n=4).

	Biomass Remaining (%)	$ke_{\ (}y^{-1}$)	$k_{s\ (}y^{-1})^a$	$k_{f\ (}y^{-1})^a$	$m_f{}^a$	$k_{s\ (}y^{-1})^b$	$k_{f\ (}y^{-1})^b$	$m_f{}^b$
Red Alder Overstory								
Red alder litter	46 ±0.7	0.64 ±0.02	0.24 ±0.01	20.6 ±1.91	0.31 ±0.01	0.27 ±0.02	24.3 ±1.63	0.28 ±0.01
Low-N Douglas-fir (DF1)	56 ±1.06	0.31 ±0.02	0.22 ±0.02	64.6 ±16.6	0.11 ±0.03	..	..	..
High-N Douglas-fir (DF7)	69 ±1.6	0.21 ±0.03	0.16 ±0.01	40.3 ±13.6	0.07 ±0.01	..	..	..
Unfertilized Plots under Douglas-fir Overstory								
Red alder litter	56 ±1.4	0.49 ±0.02	0.18 ±0.02	38.3 ±2.06	0.25 ±0.01	0.15 ±0.03	30.8 ±3.65	0.28 ±0.01
Low-N Douglas-fir (DF1)	56 ±0.4	0.29 ±0.02	0.28 ±0.01	122 ±0.00	0.03 ±0.01	..	..	..
High-N Douglas-fir (DF7)	63 ±1.5	0.21 ±0.02	0.22 ±0.02	122 ±0.00	0.02 ±0.01	..	..	..
Fertilized Plots under Douglas-fir Overstory								
Red alder litter	54 ±1.7	0.51 ±0.02	0.20 ±0.02	27.8 ±2.58	0.28 ±0.01	0.18 ±0.03	20.8 ±2.59	0.28 ±0.01
Low-N Douglas-fir (DF1)	65 ±1.4	0.29 ±0.02	0.17 ±0.01	32.6 ±15.9	0.14 ±0.02	..	..	..
High-N Douglas-fir (DF7)	68 ±1.7	0.22 ±0.03	0.15 ±0.02	34.2 ±14.6	0.10 ±0.01	..	..	..

[a] - indicates results from the unconstrained double exponential model. [b] represents results from the constrained double exponential model where the proportion of mass in the fast pool is fixed. This fixed value was generate by averaging the values for the mass proportions generated from the unconstrained model.

Table 2.5. ANOVA for percent remaining (%), single exponential equivalent k(k_e y^{-1}) and *k* slow (k_s y^{-1}) after 2 years of decomposition for low-N Douglas-fir, high-N Douglas-fir, and red alder litter compared under different overstory or fertilization treatments.

	Biomass remaining (%)	k_e (y^{-1})	k_s (y^{-1})
	Red alder vs. Douglas-fir Overstory (model 1)		
	F, *p*	F, *p*	F, *p*
Overstory (RA vs. UDF) ($F_{1,6}$, *p)*	0.37, 0.57	8.48, 0.03	0.02,0.90
Source ($F_{2,12}$, *p*)	22.87, 0.001	246.17, <0.0001	9.96, 0.003
Overstory*Source ($F_{2,12}$, *p*)	6.61, 0.01	11.93, 0.0014	3.65, 0.06
	Red alder Overstory vs. fertilized plots under Douglas-fir Overtory (model 2)		
	F, *p*	F, *p*	F, *p*
Fertilization (RA vs.FDF) ($F_{1,6}$, *p)*	4.08, 0.09	6.26, 0.05	1.01, 0.35
Source ($F_{2,12}$, *p*)	27.26, 0.001	209.19, <.0001	3.30, 0.07
Fertilization*Source ($F_{2,12}$, *p*)	2.6, 0.12	7.89, 0.007	1.14, 0.35
	Unfertilized vs. fertilized plots under Douglas-fir Overstory (model 3)		
	F, *p*	F, *p*	F, *p*
Fertilization (UDF vs. FDF) ($F_{1,3}$, *p)*	6.72, 0.08	1.15, 0.36	1.91, 0.26
Source ($F_{2,12}$, *p*)	13.5, 0.008	163.25, <.0001	4.99, 0.03
Fertilization*Source ($F_{2,12}$, *p*)	3.9, 0.05	0.28, 0.76	0.38, 0.69

Table 2.6. Differences for percent biomass remaining (%) among litter sources and overstory and fertilization treatments based on statistical models comparing decomposition under statistical model 1 (red alder and Douglas-fir overstory (all unfertilized plots)), model 2 (red alder overstory vs. fertilized plots under Douglas-fir overstory) and model 3 (unfertilized vs. fertilized plots under Douglas-fir overstory). Results for model 2 only show differences between litter sources averaged across site treatment, because no site by source interaction was detected (Table 2.5).

Statistical Model 1 (Table 2.5 ANOVA indicates effects of source, and interactions between source and treatment)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter under unfertilized Douglas-fir plots	-7.1	-16.06	1.85	-2.2	0.05
Low-N DF vs. RA litter under unfertilized Douglas-fir plots	-0.2	-9.18	8.76	-0.07	0.94
High-N DF vs. RA litter under unfertilized Douglas-fir plots	6.89	-2.07	15.85	2.14	0.05
Low-N vs. high-N DF litter under red alder plots	-13.41	-22.37	-4.45	-4.16	0
Low-N DF vs. RA litter under red alder plots	9.91	0.95	18.87	3.07	0.01
High-N DF vs. RA litter under red alder plots	23.32	14.36	32.29	7.23	<0.0001
Low-N DF - unfertilized plots under Douglas-fir vs. red alder plots	-0.03	-9.18	9.25	-0.01	0.99
High-N DF - unfertilized plots under Douglas-fir vs. red alder plots	-6.33	-15.61	2.94	-1.9	0.08
RA litter - unfertilized plots under Douglas-fir vs. red alder plots	10.09	0.83	19.37	3.03	0.01

Statistical Model 2 (Table 2.5 ANOVA indicates effect of source, no interaction or fertilization treatment effect)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter	-8.23	-15.23	-1.22	-3.26	0.007
Low-N DF vs. RA litter	10.35	3.35	17.36	4.11	0.002
High-N DF vs. RA litter	18.58	11.57	25.59	7.37	<0.001

Statistical Model 3 (Table 2.5 ANOVA indicates interaction between source and treatment)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter under unfertilized Douglas-fir plots	-7.1	-14.94	0.73	-2.52	0.03
Low-N DF vs. RA litter under unfertilized Douglas-fir plots	-0.21	-8.05	7.62	-0.08	0.94
High-N DF vs. RA litter under unfertilized Douglas-fir plots	6.89	-0.95	14.73	2.44	0.03
Low-N vs. high-N DF litter under fertilized Douglas-fir plots	-3.04	-10.88	4.79	-1.08	0.3
Low-N DF vs. RA litter under fertilized Douglas-fir plots	10.79	2.96	18.63	3.38	0.002
High-N DF vs. RA litter under fertilized Douglas-fir plots	13.84	5.99	21.67	4.9	0.004
Low-N DF - unfertilized vs. fertilized plots under Douglas-fir	-9.25	-17.08	-1.41	-3.28	0.007
High-N DF - unfertilized vs. fertilized plots under Douglas-fir	-5.18	-13.02	2.66	-1.84	0.09
RA litter - fertilized vs. fertilized plots under Douglas-fir	1.76	-6.07	9.6	0.63	0.54

Table 2.7. Differences for single exponential equivalent *k* (k_e (y^{-1})) among litter sources and overstory and fertilization treatments based on statistical models comparing decomposition under statistical model 1 (red alder and Douglas-fir overstory (all unfertilized plots)), model 2 (red alder overstory vs. fertilized plots under Douglas-fir overstory) and model 3 (unfertilized vs. fertilized plots under Douglas-fir overstory). Results for model 3 only show differences between litter sources averaged across site treatment, because no site by source interaction was detected (Table 2.5).

Statistical Model 1 (Table 2.5 ANOVA indicates interaction between source and treatment)

Comparison of single exponential equivalent k	Difference	lower 95% CI	upper 95% CI	T Value	Pr > |t|
Low-N vs. high-N DF litter under unfertilized Douglas-fir plots	0.08	0.01	0.14	3.4	0.005
Low-N DF vs. RA litter under unfertilized Douglas-fir plots	-0.19	-0.26	-0.14	-8.51	0.0001
High-N DF vs. RA litter under unfertilized Douglas-fir plots	-0.28	-0.34	-0.21	-11.92	0.0001
Low-N vs. high-N DF litter under red alder	0.09	0.03	0.16	4.14	0.0014
Low-N DF vs. RA litter under red alder	-0.33	-0.39	-0.26	-14.09	<0.0001
High-N DF vs. RA litter under red alder	-0.43	-0.49	-0.36	-18.23	<0.0001
Low-N DF litter under red alder vs. unfertilized Douglas-fir plots	-0.02	-0.1	0.06	-0.85	0.41
High-N DF litter under red alder vs. unfertilized Douglas-fir plots	-0.007	-0.09	0.07	-0.24	0.81
RA litter under red alder vs. unfertilized Douglas-fir plots	-0.15	-0.51	-0.35	-5.41	0.0002

Statistical Model 2 (Table 2.5 ANOVA 5 indicates effects of source, fertilization treatment, and their interaction)

Comparison of single exponential equivalent k	Difference	lower 95% CI	upper 95% CI	T Value	Pr > |t|
Low-N vs. high-N DF litter under fertilized Douglas-fir plots	0.06	-0.008	0.14	2.48	0.03
Low-N DF vs. RA litter under fertilized Douglas-fir plots	-0.22	-0.29	-0.15	-8.62	<0.0001
High-N DF vs. RA litter under fertilized Douglas-fir plots	0.03	-0.36	-0.22	-11.1	0.001
Low-N vs. high-N DF litter under red alder	0.09	0.02	0.17	3.74	0.003
Low-N DF vs. RA litter under red alder	-0.33	-0.41	-0.26	-12.73	0.001
High-N DF vs. RA litter under red alder	-0.54	-0.49	-0.35	-16.47	0.001
Low-N DF litter under red alder vs. fertilized Douglas-fir plots	-0.02	-0.1	0.06	-0.82	0.43
High-N DF litter under red alder vs. fertilized Douglas-fir plots	0.01	-0.07	0.09	0.34	0.74
RA litter under red alder vs. fertilized Douglas-fir plots	-0.13	-0.21	-0.05	-4.55	0.0007

Statistical Model 3 (Table 2.5 ANOVA indicates effects of source only)

Comparison of single exponential equivalent k	Difference	lower 95% CI	upper 95% CI	T Value	Pr > |t|
Low-N vs. high-N DF litter	0.07	0.03	0.12	4,41	0.0008
Low-N DF vs. RA litter	-0.21	-0.26	-0.16	-12.97	<0.0001
High-N DF vs. RA litter	-0.28	-0.33	-0.21	-12.4	<0.0001

Table 2.8. Results from MANOVA for unconstrained double exponential models. The unconstrained double exponential model parameters included decomposition rates (k_s (y^{-1}) and k_f, (y^{-1})) and the proportion of litter in fast pool, m_f.

Model 1	**Red alder vs. Douglas-fir Overstory**
	F, *p*
Overstory (RA vs. UDF) ($F_{1,6}$, *p)*	10.93, 0.004
Source ($F_{2,12}$, *p*)	56.82, <0.001
Overstory*Source ($F_{2,12}$, *p*)	0.21, 0.81
Model 2	**Red alder Overstory vs. fertilized plots under Douglas-fir Overstory**
	F, *p*
Fertilization (RA vs.FDF) ($F_{1,6}$, *p)*	0.02, 0.90
Source ($F_{2,12}$, *p*)	22.10, <0.0001
Fertilization*Source ($F_{2,12}$, *p*)	0.96, 0.41
Model 3	**Unfertilized vs. fertilized plots under Douglas-fir Overstory**
	F, *p*
Fertilization (UDF vs. FDF) ($F_{1,3}$, *p)*	13.84, 0.002
Source ($F_{2,12}$, *p*)	44.98, <0.0001
Fertilization*Source ($F_{2,12}$, *p*)	2.66, 0.09

Table 2.9. Results from ANOVA comparing the proportion of mass in the fast and slow pools from the unconstrained double exponential model.

Model 1	**Red alder vs. Douglas-fir Overstory**
	F, *p*
Overstory (RA vs. UDF) ($F_{1,6}$, *p)*	5.08, 0.07
Source ($F_{2,12}$, *p*)	128.18, <0.0001
Overstory*Source ($F_{2,12}$, *p*)	0.50, 0.62

Model 2	**Red alder Overstory vs. fertilized plots under Douglas-fir Overstory**
	F, *p*
Fertilization (RA vs. FDF) ($F_{1,6}$, *p)*	0.01, 0.94
Source ($F_{2,12}$, *p*)	51.57, <0.0001
Fertilization*Source ($F_{2,12}$, *p*)	2.18, 0.16

Model 3	**Unfertilized vs. fertilized plots under Douglas-fir Overstory**
	F, *p*
Fertilization (UDF vs. FDF) ($F_{1,3}$, *p)*	11.07, 0.04
Source ($F_{2,12}$, *p*)	108.99, <0.0001
Fertilization*Source ($F_{2,12}$, *p*)	6.61, 0.013

Table 2.10. Differences for decomposition mass proportion of slow and fast pools for red alder and low-N and high-N Douglas-fir litter based on statistical models comparing decomposition under statistical model 1 (red alder and Douglas-fir overstory (all unfertilized plots)), model 2 (red alder overstory vs. fertilized plots under Douglas-fir overstory) and model 3 (unfertilized vs. fertilized plots under Douglas-fir overstory). For models 1 and 2, source was significant and differences are presented below. For model 3, there was an interaction between source and site treatment with the differences presented below.

Statistical Model 1 (Table 2.9 ANOVA indicates effect of source, no interaction or fertilization treatment effect)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter	0.03	-0.02	0.07	1.53	0.15
Low-N DF vs. RA litter	-0.21	-0.25	-0.16	-13.04	<.0001
High-N DF vs. RA litter	-0.23	-0.27	-0.19	-14.57	<.0001

Statistical Model 2 (Table 2.9 ANOVA indicates effect of source, no interaction or fertilization treatment effect)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter	0.04	-0.02	0.01	2.04	0.06
Low-N DF vs. RA litter	-0.16	-0.22	-0.1	-7.6	<.0001
High-N DF vs. RA litter	-0.2	-0.26	-0.14	-9.64	<.0001

Statistical Model 3 (Table 2.9 ANOVA indicates interaction between source and treatment)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter under unfertilized Douglas-fir plots	0.009	-0.05	0.07	0.46	0.65
Low-N DF vs. RA litter under unfertilized Douglas-fir plots	-0.22	-0.28	-0.17	-10.79	<.0001
High-N DF vs. RA litter under unfertilized Douglas-fir plots	-0.23	-0.29	-0.17	-11.26	<.0001
Low-N vs. high-N DF litter under fertilized Douglas-fir plots	0.05	-0.01	0.1	2.21	0.05
Low-N DF vs. RA litter under fertilized Douglas-fir plots	-0.12	-0.18	-0.06	-5.8	<.0001
High-N DF vs. RA litter under fertilized Douglas-fir plots	-0.17	-0.22	-0.11	-8.01	<.0001
Low-N DF - unfertilized vs. fertilized plots under Douglas-fir	-0.11	-0.18	-0.04	-4.39	0.0009
High-N DF - unfertilized vs. fertilized plots under Douglas-fir	-0.08	-0.15	-0.006	-3	0.01
RA litter - fertilized vs. fertilized plots under Douglas-fir	-0.01	-0.08	0.06	-0.42	0.68

Table 2.11. Results from ANOVA comparing rate of fast pool, k_{fast} **(y^{-1})** from the unconstrained double exponential model.

Model 1	**Red alder vs. Douglas-fir Overstory**
	F, *p*
Overstory (RA vs. UDF) ($F_{1,6}$, *p)*	7.11, 0.04
Source ($F_{2,12}$, *p*)	12.60, 0.001
Overstory*Source ($F_{2,12}$, *p*)	2.87, 0.09

Model 2	**Red alder Overstory vs. fertilized plots under Douglas-fir Overstory**
	F, *p*
Fertilization (RA vs. FDF) ($F_{1,6}$, *p)*	0.13, 0.73
Source ($F_{2,12}$, *p*)	1.01, 0.39
Fertilization*Source ($F_{2,12}$, *p*)	0.67, 0.53

Model 3	**Unfertilized vs. fertilized plots under Douglas-fir Overstory**
	F, *p*
Fertilization (UDF vs. FDF) ($F_{1,3}$, *p)*	10.2, 0.04
Source ($F_{2,12}$, *p*)	11.14, 0.002
Fertilization*Source ($F_{2,12}$, *p*)	8.52, 0.005

Table 2.12. Differences for decomposition of fast pool (k_{fast} **(y^{-1})**) for red alder and low-N and high-N Douglas-fir litter based on statistical models comparing decomposition under statistical model 1 (red alder and Douglas-fir overstory (all unfertilized plots)), model 2 (red alder overstory vs. fertilized plots under Douglas-fir overstory) and model 3 (unfertilized vs. fertilized plots under Douglas-fir overstory). For models 1, source and site treatment were significant and differences are presented below. For models 2, there was an interaction between source and site treatment and differences are presented below. For model 3, there was no source effect, treatment effect, or interaction so no differences are presented.

Statistical Model 1 (Table 2.11 ANOVA indicates effects of source and site treatment, but no interaction)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter under unfertilized Douglas-fir plots	-7.00E-18	-53.03	53.02	0	1
Low-N DF vs. RA litter under unfertilized Douglas-fir plots	83.65	30.63	136.68	4.38	0.0009
High-N DF vs. RA litter under unfertilized Douglas-fir plots	83.65	30.63	136.68	4.38	0.0009
Low-N vs. high-N DF litter under red alder	24.33	-28.69	77.35	1.27	0.23
Low-N DF vs. RA litter under red alder	43.96	-9.07	96.99	2.3	0.04
High-N DF vs. RA litter under red alder	19.63	-33.39	72.66	1.03	0.32
Low-N DF litter under red alder vs. unfertilized Douglas-fir plots	57.39	-12.18	126.97	2.29	0.05
High-N DF litter under red alder vs. unfertilized Douglas-fir plots	81.72	12.15	151.29	3.26	0.007
RA litter under red alder vs. unfertilized Douglas-fir plots	17.69	-51.88	87.27	0.71	0.49

Statistical Model 2 (Table 2.11 ANOVA indicates interaction between source and site treatment)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
No significant effects					

Statistical Model 3 (Table 2.11 ANOVA indicates no effect of source, site treatment or interactions)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter under unfertilized Douglas-fir plots	-8.00E-17	-42.91	42.91	0	1
Low-N DF vs. RA litter under unfertilized Douglas-fir plots	83.66	40.75	126.56	5.42	0.0002
High-N DF vs. RA litter under unfertilized Douglas-fir plots	83.66	40.75	126.56	5.42	0.0002
Low-N vs. high-N DF litter under fertilized Douglas-fir plots	-1.61	-44.52	41.29	-0.1	0.92
Low-N DF vs. RA litter under fertilized Douglas-fir plots	4.79	-38.11	47.7	0.31	0.76
High-N DF vs. RA litter under fertilized Douglas-fir plots	6.41	-36.49	49.31	0.41	0.69
Low-N DF - unfertilized vs. fertilized plots under Douglas-fir	89.37	24.65	154.09	3.74	0.002
High-N DF - unfertilized vs. fertilized plots under Douglas-fir	87.86	23.04	152.48	3.77	0.002
RA litter - fertilized vs. fertilized plots under Douglas-fir	10.51	-54.21	75.23	0.45	0.66

Table 2.13. Results from ANOVA comparing decomposition of slow pool (k_{slow} **(y^{-1}))** from the unconstrained double exponential model.

Model 1	**Red alder vs. Douglas-fir Overstory**
	F, *p*
Overstory (RA vs. UDF) ($F_{1,6}$, *p)*	0.54, 0.49
Source ($F_{2,12}$, *p*)	3.48, 0.06
Overstory*Source ($F_{2,12}$, *p*)	3.69, 0.06

Model 2	**Red alder Overstory vs. fertilized plots under Douglas-fir Overstory**
	F, *p*
Fertilization (RA vs. FDF) ($F_{1,6}$, *p)*	0.86, 0.39
Source ($F_{2,12}$, *p*)	2.99, 0.09
Fertilization*Source ($F_{2,12}$, *p*)	0.53, 0.60

Model 3	**Unfertilized vs. fertilized plots under Douglas-fir Overstory**
	F, *p*
Fertilization (UDF vs. FDF) ($F_{1,3}$, *p)*	3.94,0.14
Source ($F_{2,12}$, *p*)	1.71, 0.22
Fertilization*Source ($F_{2,12}$, *p*)	4.07, 0.04

Table 2.14. Differences for decomposition of slow pool (k_{slow} **(y^{-1}))** for red alder and low-N and high-N Douglas-fir litter based on statistical models comparing decomposition under statistical model 1 (red alder and Douglas-fir overstory (all unfertilized plots)), model 2 (red alder overstory vs. fertilized plots under Douglas-fir overstory) and model 3 (unfertilized vs. fertilized plots under Douglas-fir overstory). For models 1 and 2, there were no significant effects. For model 3, there was an interaction between source and site treatment and the differences are presented.

Statistical Model 1 (Table 2.13 ANOVA indicates no effects source, site treatment, or interaction)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
No significant effects					

Statistical Model 2 (Table 2.13 ANOVA indicates effect of source, no interaction or fertilization treatment effect)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
No significant effects					

Statistical Model 3 (Table 2.13 ANOVA indicates interaction between source and treatment)

Comparison of percent biomass remaining	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter under unfertilized Douglas-fir plots	0.06	-0.02	0.015	2	0.07
Low-N DF vs. RA litter under unfertilized Douglas-fir plots	0.09	0.008	0.18	3.05	0.01
High-N DF vs. RA litter under unfertilized Douglas-fir plots	0.03	-0.07	0.12	1.04	0.32
Low-N vs. high-N DF litter under fertilized Douglas-fir plots	0.01	-0.07	0.1	0.4	0.7
Low-N DF vs. RA litter under fertilized Douglas-fir plots	-0.03	-0.12	0.06	-0.96	0.36
High-N DF vs. RA litter under fertilized Douglas-fir plots	-0.04	-0.13	0.04	-1.36	0.2
Low-N DF - unfertilized vs. fertilized plots under Douglas-fir	0.11	0.009	0.21	3.02	0.01
High-N DF - unfertilized vs. fertilized plots under Douglas-fir	0.06	-0.04	0.016	1.62	0.13
RA litter - fertilized vs. fertilized plots under Douglas-fir	-0.02	-0.12	0.09	-0.41	0.69

Table 2.15. N Dynamics in decomposed litter after 2 years. Error represents standard error calculated for each overstory or fertilization treatment (n=4).

Source	Initial Values		Values after two years of decomposition			
	Initial N mg/g	Initial C:N	N mg/g	N (mg) Immobilized: g initial litter†	% Initial N*	C:N
Red alder Overstory (RA)						
Low-N Douglas-fir litter	6.8	76	21.7 ±1.63	5.41 ±1.33	180 ±19.8	22 ±1.6
High-N Douglas-fir litter	12.2	44	17.0 ±2.26	-0.32 ±1.79	97 ±14.8	31 ±2.3
Red alder litter	23.4	23	16.1 ±1.01	-16.08 ±0.61	31 ±2.59	32 ±1.7
Douglas-fir Overstory (UDF)						
Low-N Douglas-fir litter	6.8	76	18.3 ±2.33	3.43 ±1.37	151 ±20.1	28 ±3.1
High-N Douglas-fir litter	12.2	44	22.4 ±0.24	-0.93 ±0.31	92 ±2.5	28 ±1.8
Red alder litter	23.4	23	19.6 ±2.26	-12.43 ±1.60	47 ±6.8	27 ±3.1
Douglas-fir Overstory (FDF)						
Low-N Douglas-fir litter	6.8	76	16.9 ±0.80	4.23 ±0.93	163 ±13.9	30 ±1.6
High-N Douglas-fir litter	12.2	44	22.4 ±0.48	3.06 ±0.92	125 ±7.6	23 ±0.4
Red alder litter	23.4	23	22.6 ±3.43	-11.16 ±2.26	53 ±9.65	24 ±3.5

note: † Negative value indicates net N mineralization.

* Values over 100% indicate net immbolization and values under 100% indicate mineralization.

* Percent of initial is relative to the initial value, i.e. at the onset of the experiment, the amount of N is 100% of initial.

Table 2.16. Results from ANOVA comparing the N immobilization after 2 years of decomposition.

N Immobilization

Model 1	**Red alder vs. Douglas-fir Overstory**
	F, *p*
Overstory (RA vs. UDF) ($F_{1,6}$, *p)*	0.32, 0.59
Source ($F_{2,12}$, *p*)	45.97, <0.001
Overstory*Source ($F_{2,12}$, *p*)	1.45, 0.27

Model 2	**Red alder Overstory vs. fertilized plots under Douglas-fir Overstory**
	F, *p*
Fertilization (RA vs. FDF) ($F_{1,6}$, *p)*	0.86, 0.39
Source ($F_{2,12}$, *p*)	58.40, <0.001
Fertilization*Source ($F_{2,12}$, *p*)	2.06, 0.17

Model 3	**Unfertilized vs. fertilized plots under Douglas-fir Overstory**
	F, *p*
Fertilization (UDF vs. FDF) ($F_{1,3}$, *p)*	3.82, 0.15
Source ($F_{2,12}$, *p*)	52.41, <0.001
Fertilization*Source ($F_{2,12}$, *p*)	0.94, 0.42

Table 2.17. Differences for N immobilization among litter sources and overstory and fertilization treatments based on statistical models comparing decomposition under statistical model 1 (red alder and Douglas-fir overstory (all unfertilized plots)), model 2 (red alder overstory vs. fertilized plots under Douglas-fir overstory) and model 3 (unfertilized vs. fertilized plots under Douglas-fir overstory). Results for models only show differences between litter sources averaged across site treatment, because no site by source interaction was detected (Table 2.14).

Statistical Model 1 (indicates litter source effect, no treatment effect or interaction)

Comparison of N immobilization	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter	70.61	33.93	107.29	5.35	0.0002
Low-N DF vs. RA litter	126.29	89.61	162.97	9.57	< 0.0001
High-N DF vs. RA litter	55.68	18.99	92.35	4.22	0.0012

Statistical Model 2 (indicates no litter source or treatment effect or interaction)

Comparison of N immobilization	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter	60.11	26.79	93.44	5.01	0.0003
Low-N DF vs. RA litter	129.51	96.19	162.84	10.8	<0.0001
High-N DF vs. RA litter	69.4	36.08	102.73	5.79	<0.0001

Statistical Model 3 (indicates litter source effect, no treatment effect or interaction)

Comparison of N immobilization	Difference	lower 95% CI	upper 95% CI	t Value	Pr > |t|
Low-N vs. high-N DF litter	48.03	18.92	77.13	4.58	0.0006
Low-N DF vs. RA litter	107.08	77.97	136.18	10.22	<0.001
High-N DF vs. RA litter	59.05	29.94	88.16	5.64	0.0001

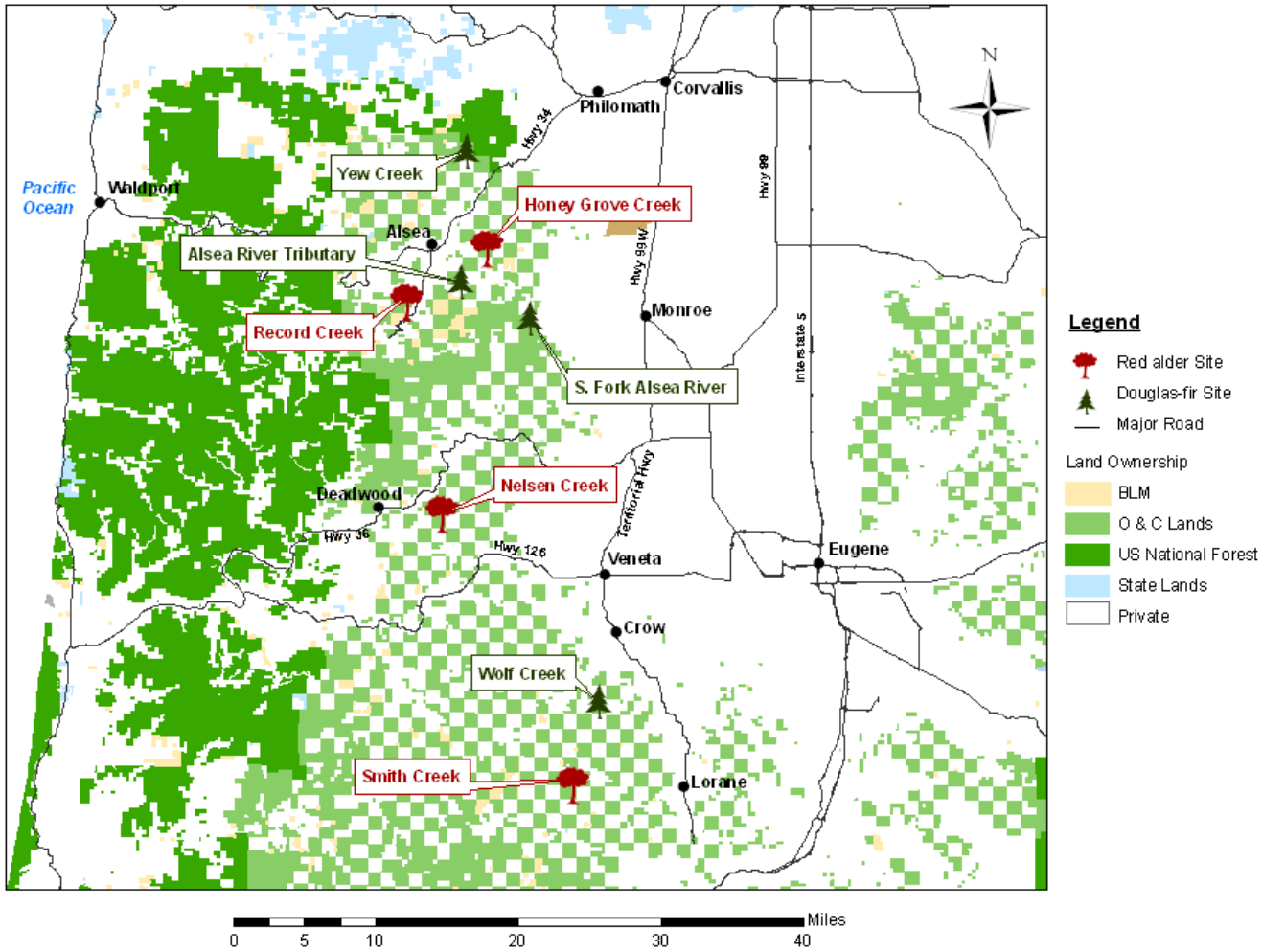

Figure 2.1. Site Map.

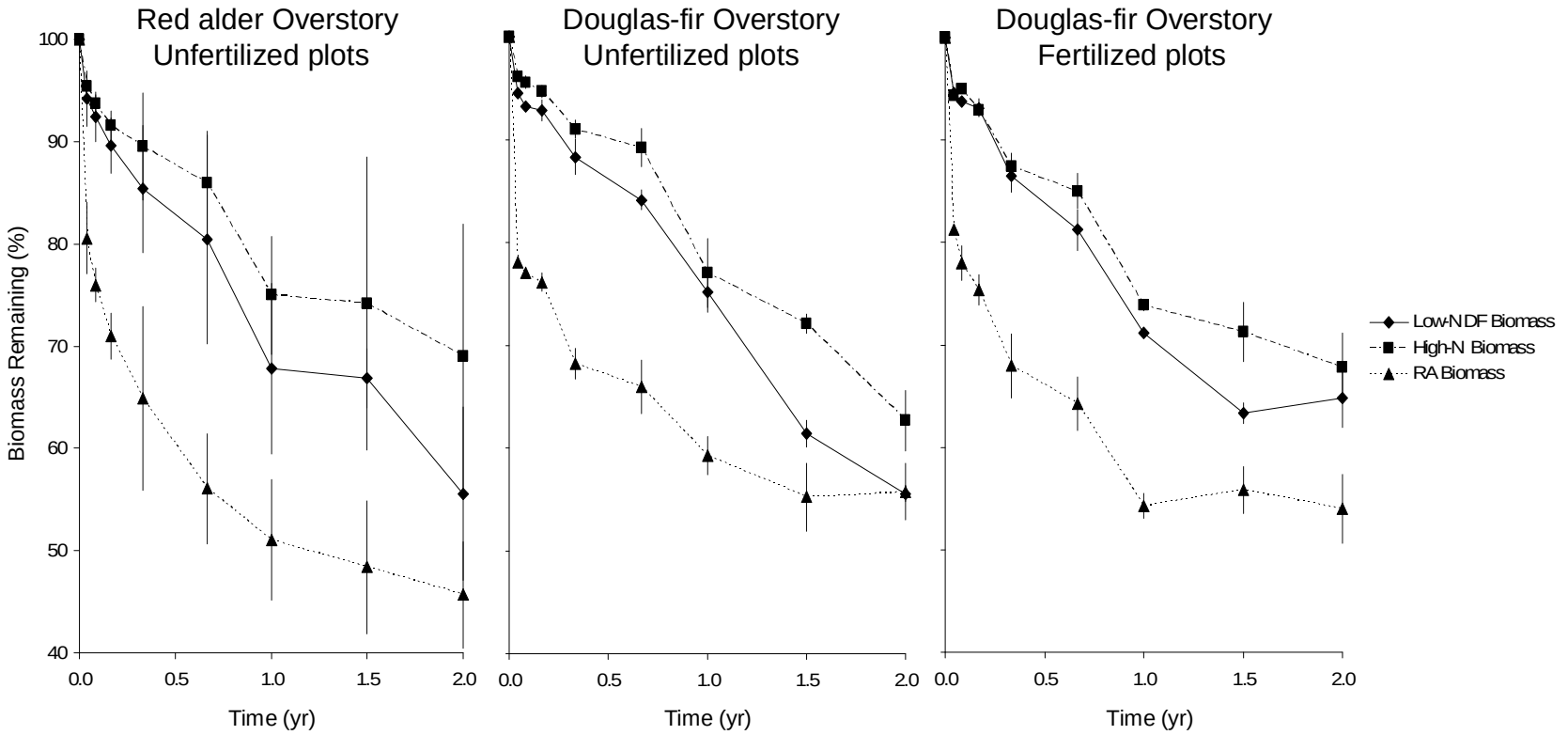

Figure 2.2. Biomass remaining from red alder, low-N Douglas-fir, and high-N Douglas-fir leaf litter decomposition from plots under red alder overstory and from unfertilized and fertilized plots under Douglas-fir overstory. Each point represents the average of the 4 overstory or fertilization treatment replications. Error bars represent standard error calculated for each overstory or fertilization treatment (n=4). Bags were placed in field in November 2003 with last collection in November 2005.

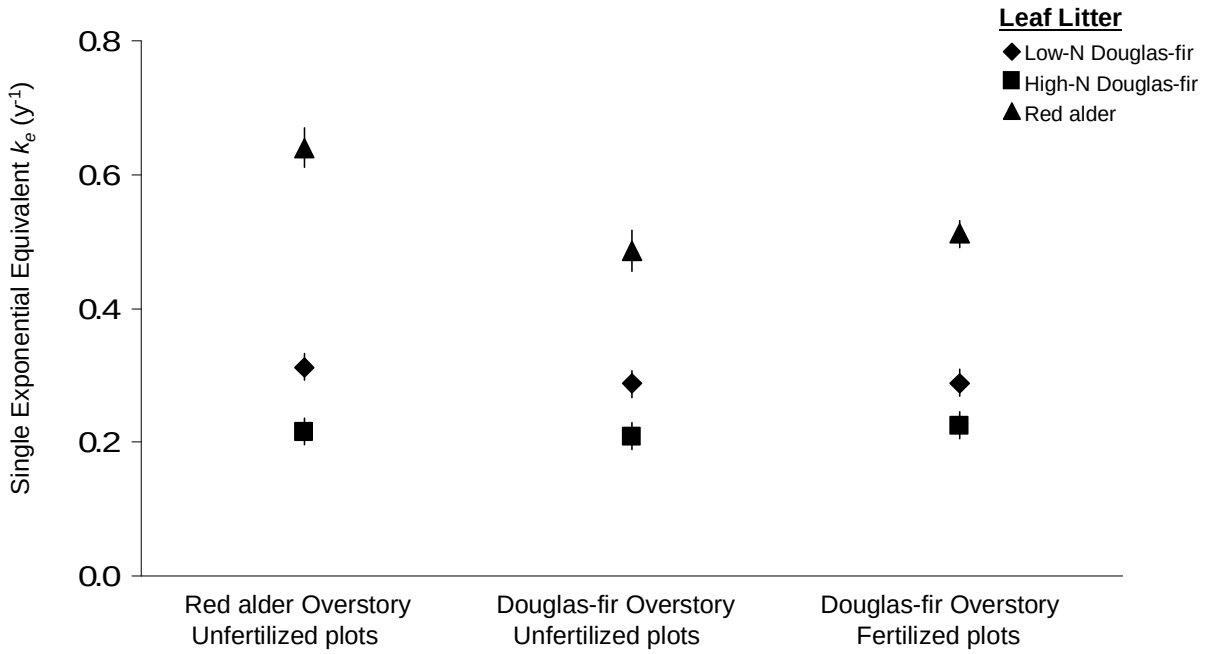

Figure 2.3. Single exponential equivalent *k* (k_e) calculated after 2 years of decomposition for red alder, low-N Douglas-fir, and high-N Douglas-fir leaf litter decomposition from plots under red alder overstory and from unfertilized and fertilized plots under Douglas-fir overstory. Each point represents the average of the 4 overstory or fertilization treatment replications. Error bars represent standard error calculated for each overstory or fertilization treatment (n=4).

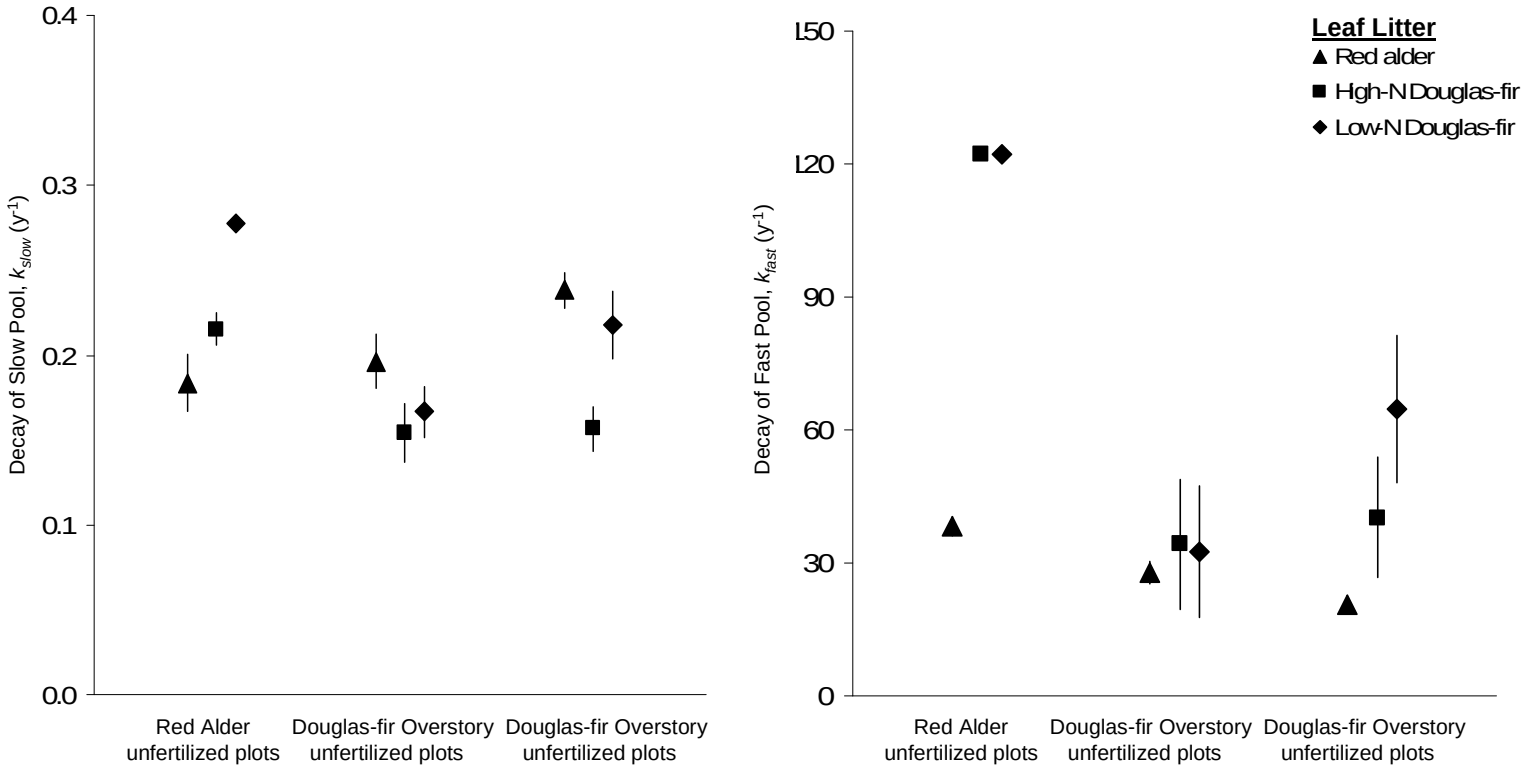

Figure 2.4. Decomposition rates as determined by the unconstrained double exponential. Each point represents the average of the 4 overstory or fertilization treatment replications. Error bars represent standard error calculated for each overstory or fertilization treatment (n=4). Bags were placed in field in November 2003 with last collection in November 2005. In the case of the fast pool decomposing under red alder, error bars are not visible. In the case of red alder, the error was smaller than the size of the triangle. In the case of both Douglas-fir litter sources, the fast pool was constrained at 122 (y-1) because when unconstrained, the rate is exponentially high. The value of 122 is the amount all of the material would have decomposed in the first collection interval.

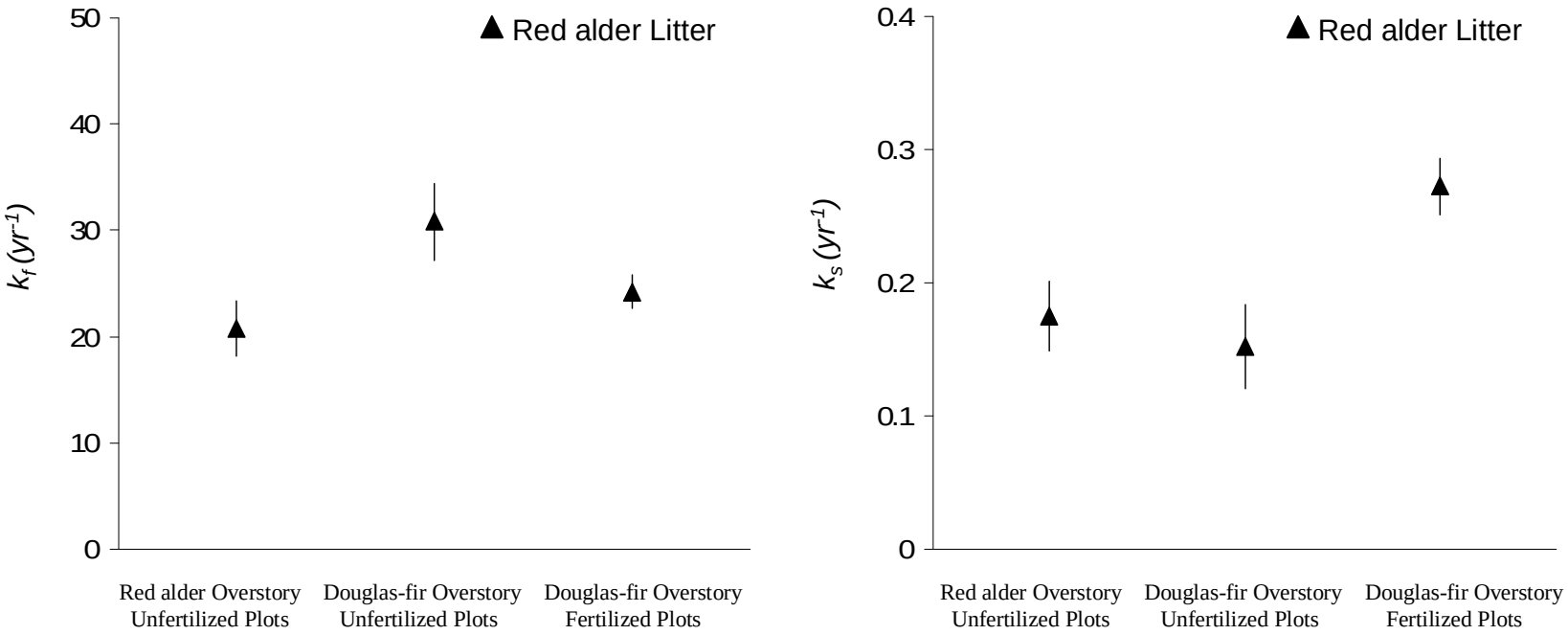

Figure 2.5. Decomposition rates as determined by the constrained double exponential model in which the pool size is pre-defined (28% in the fast pool) and the rates are estimated by the model from red alder litter decomposed in plots under red alder overstory and from unfertilized and fertilized plots under Douglas-fir overstory. Each point represents the average of the 4 overstory or fertilization treatment replications. Error bars represent standard error calculated for each overstory or fertilization treatment (n=4). Bags were placed in field in November 2003 with last collection in November 2005.

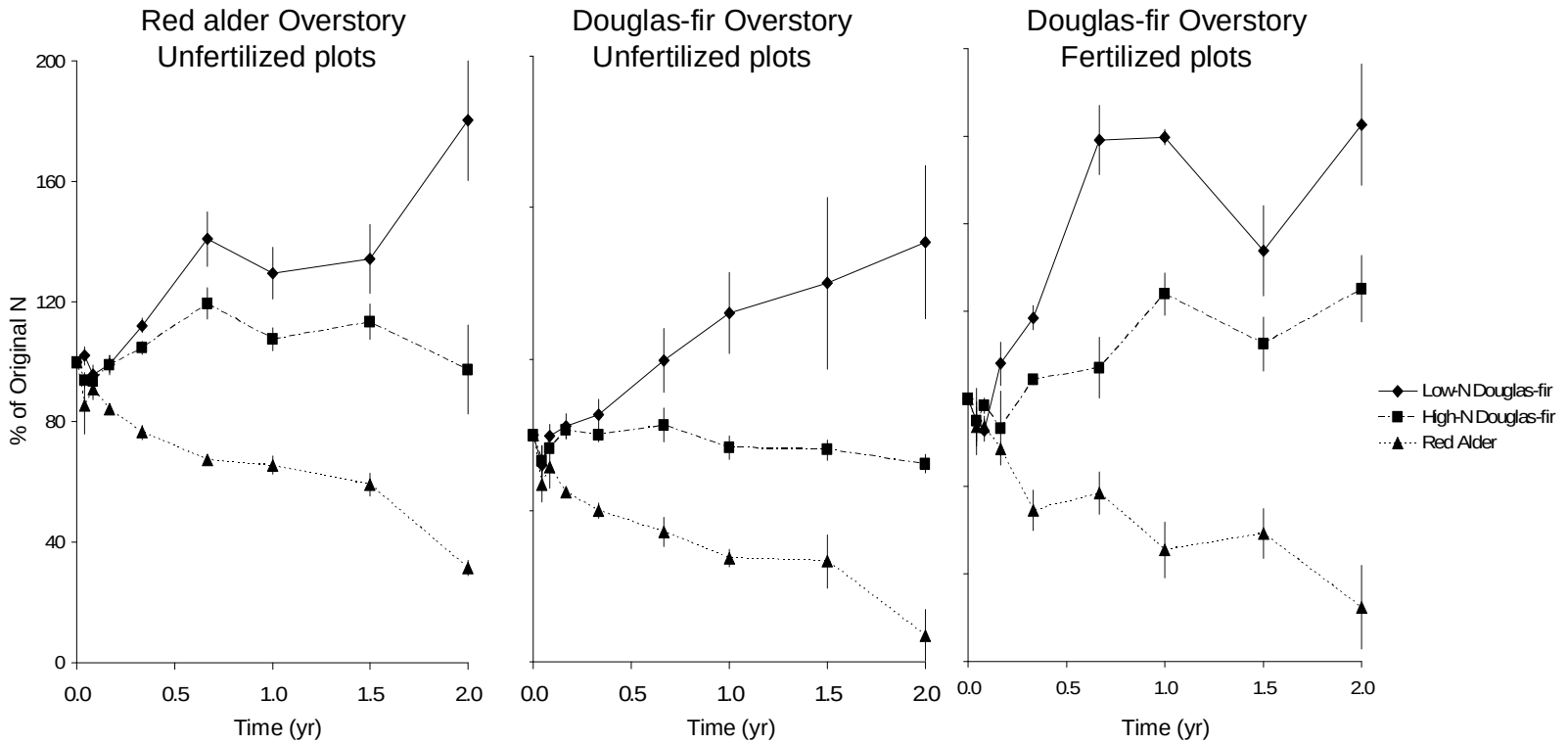

Figure 2.6. Percent N of initial value from red alder, low-N Douglas-fir, and high-N Douglas-fir leaf litter decomposition from plots under red alder overstory and from unfertilized and fertilized plots under Douglas-fir overstory. Each point represents the average of the 4 overstory or fertilization treatment replications. Error bars represent standard error calculated for each overstory or fertilization treatment (n=4). Bags were placed in field in November 2003 with last collection in November 2005.

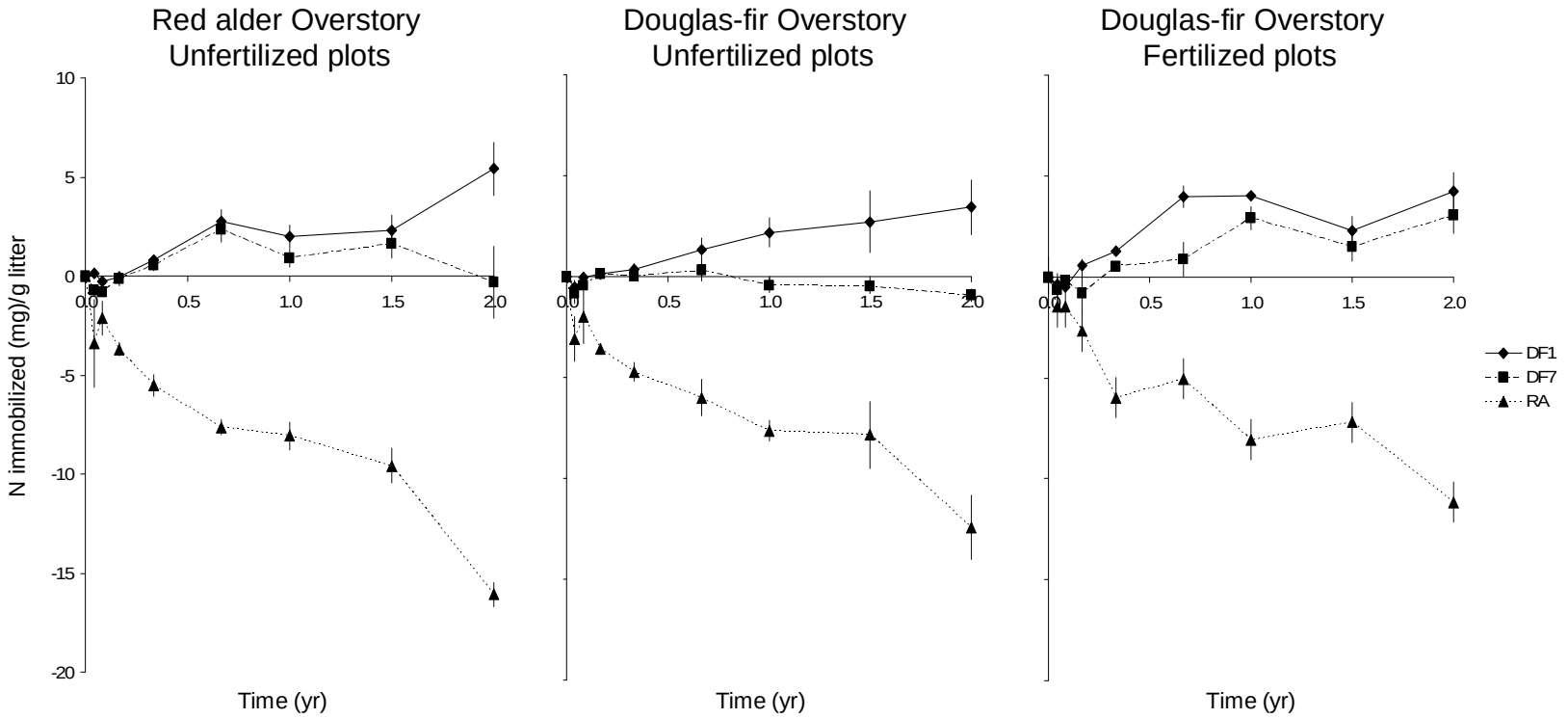

Figure 2.7. N(mg) immobilized per gram of initial litter in red alder, low-N Douglas-fir, and high-N Douglas-fir leaf litter decomposition from plots under red alder overstory and from unfertilized and fertilized plots under Douglas-fir overstory. Each point represents the average of the 4 overstory or fertilization treatment replications. Error bars represent standard error calculated for each overstory or fertilization treatment (n=4). Bags were placed in field in November 2003 with last collection in November 2005.

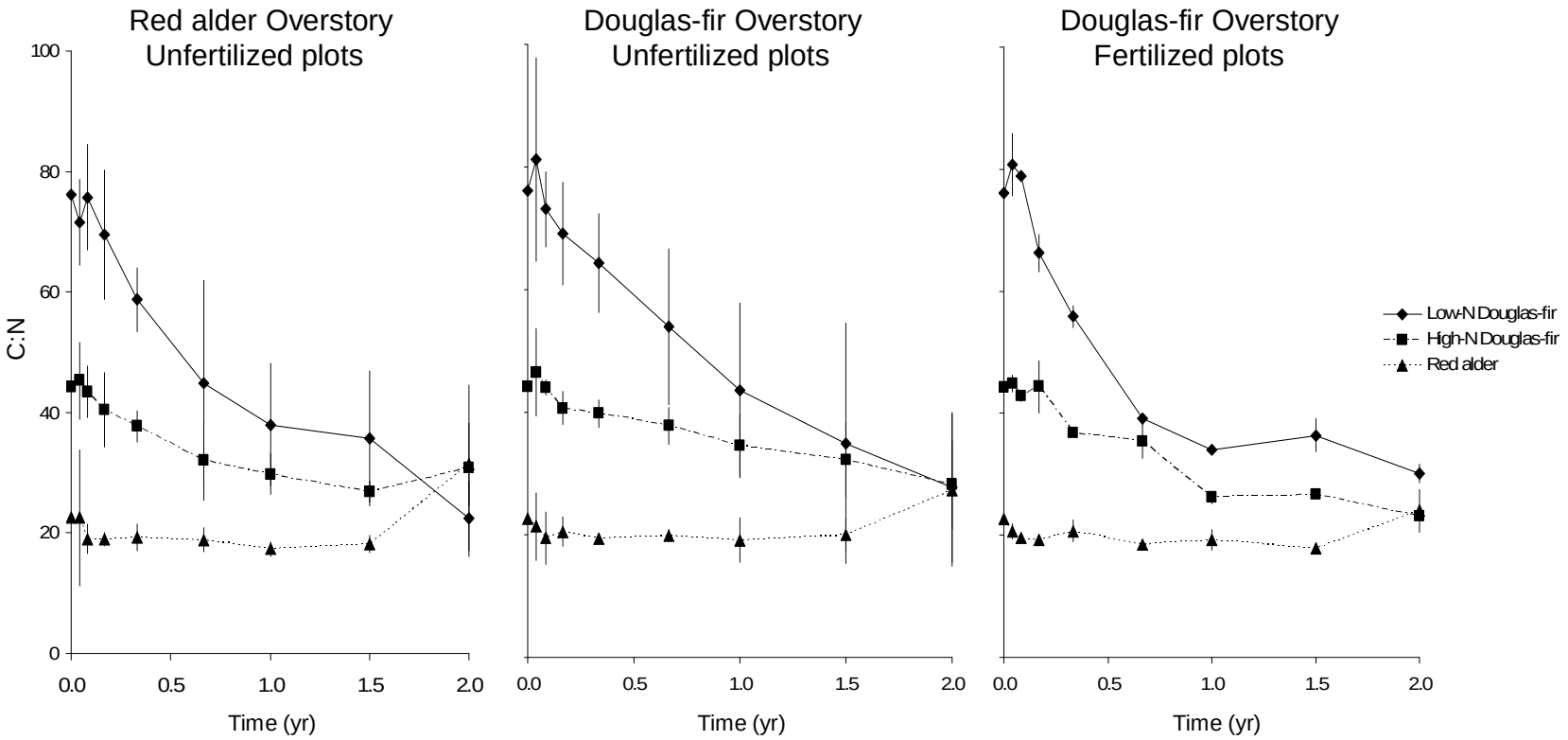

Figure 2.8. C:N ratio of red alder leaves, low-N, and high-N Douglas-fir leaf litter from plots under red alder overstory and from unfertilized and fertilized plots under Douglas-fir overstory. Each point represents the average of the 4 overstory or fertilization treatment replications. Error bars represent standard error calculated for each overstory or fertilization treatment (n=4). Bags were placed in field in November 2003 with last collection in November 2005.

Table 3.1. Site, location, elevation and soil characterization of the 8 research sites (4 dominated by red alder and 4 by Douglas-fir) NRCS Online Soil Survey

Site	Riparian Overstory	Location	Elevation (m)	Soil series of stream and surrounding area	Classification
Honey Grove Creek					
	Red alder	44° 20'N, 123° 38' W	139	Elsie silt loam	Silty alluvium derived from sandstone
				Treharne-Eilertsen-Zyzzug complex	Silty alluvium derived from sandstone
Nelson Creek					
	Red alder	44° 36'N, 123° 36' W	165	Meda loam	Alluvium and colluvium derived from sandstone
				Preacher loam	Colluvium and residuum derived from sandstone
Smith Creek					
	Red alder	43° 50'N, 123° 22' W	263	Peavine silty clay loam	Colluvium and residuum derived from sandstone
				Digger-Bohannon complex	Colluvium and residuum derived from sandstone
				Bohannon gravelly loam	Colluvium derived from sandstone
Record Creek					
	Red alder	44° 20'N, 123° 38' W	137	Treharne-Eilertsen-Zyzzug complex	Silty alluvium derived from sandstone
				Meda-Treharne-Wasson complex	Loamy alluvium and colluvium derived from sandstone
					Silty alluvium derived from sandstone
Alsea River Tributary					
	Douglas-fir	44° 19'N, 123° 28' W	284	Bohannon-Preacher complex	Colluvium and residuum derived from sandstone
				Nekoma-Fluvaquents complex	Recent loamy alluvium derived from sandstone
S. Fork Alsea Tributary					
	Douglas-fir	44° 21'N, 123° 34' W	299	Honeygrove-Shivigny complex	Clayey colluvium and residuum derived from basalt
				Elsie silt loam	Silty alluvium derived from basalt
				Meda-Treharne-Wasson complex	Loamy alluvium and colluvium derived from basalt
					Silty alluvium derived from basalt
Wolf Creek					
	Douglas-fir	43° 55'N, 123° 21' W	187	Jory silty clay loam	Loamy colluvium derived from sandstone
				Eilertsen silt loam	Alluvium derived from sandstone
Yew Creek					
	Douglas-fir	44° 30'N, 123° 33' W	588	Hemcross-Klistan complex	Colluvium and residuum derived from basalt
				Meda-Treharne-Wasson complex	Loamy alluvium and colluvium derived from basalt
					Silty alluvium derived from basalt

Table 3.2. Litterfall, forest floor, and soil characteristics (n=4) for each treatment.

Site Characteristic	Unfertilized Douglas-fir	Fertilized Douglas-fir	Red alder
Litterfall			
Red alder Litterfall N (%)	2.1 ±0.03	..	2.2 ±0.03
Red alder Litterfall C (%)	52.3 ±0.28	..	52.0 ±0.06
Red alder Litterfall C:N	24.4 ±0.28	..	24.0 ±0.29
Douglas-fir Litterfall N (%)	0.8^{b} ±0.01	..	1.3^{a} ±0.14
Douglas-fir Litterfall C (%)	53.1 ±0.08	..	53.2 ±0.28
Douglas-fir Litterfall C:N	70.1^{b} ±0.76	..	43.8^{a} ±3.36
Forest Floor			
Forest Floor N (%)	1.10^{b} ±0.02	1.20^{b} ±0.06	1.66^{a} ±0.06
Forest Floor C (%)	47.92^{b} ±0.56	48.27^{b} ±0.76	41.91^{a} ±0.98
Forest Floor C:N	43.79^{b} ±1.21	41.12^{b} ±1.77	25.78^{a} ±1.35
Forest Floor $NH_4^+ + NO_3^-$ (mg/kg)	0.31^{b} ±0.06	4.14^{c} ±0.59	2.85^{a} ±0.32
Forest Floor NO_3^- (%)	7.17^{b} ±2.31	22.28^{c} ±1.50	41.56^{a} ±2.85
Forest Floor N Mineralization	0.98^{b} ±0.63	2.21^{b} ±0.45	10.28^{a} ±0.65
Forest Floor Nitrification (%)	80^{b} ±23.0	94 ±13.9	74^{a} ±2.3
Soil			
Soil N (%)	0.25 ±0.01	0.32 ±0.01	0.30 ±0.02
Soil C (%)	6.24 ±0.50	9.25 ±1.05	5.45 ±0.60
Soil C:N	24.45^{b} ±0.74	28.24^{b} ±1.99	17.92^{a} ±0.70
Soil $NH_4^+ + NO_3^-$	0.15^{a} ±0.04	0.42^{b} ±0.08	0.29^{a} ±0.03
Soil NO_3^- (%)	21.48^{b} ±1.96	51.75^{c} ±3.50	87.05^{a} ±2.07
Soil N Mineralization	0.64 ±0.21	0.58 ±0.09	0.64 ±0.06
Soil Nitrification (%)	61^{b} ±0.07	59^{ab} ±1.2	100^{a} ±na
Soil Bulk Density (g/m^3)	0.54 ±0.01	0.59 ±0.01	0.55 ±0.04
Soil Ph	6.38^{b} ±0.13	5.75^{c} ±0.15	5.32^{a} ±0.14

Notes: The reported values are the mean of the 4 site or fertilization treatment replications. Different letters indicate significant statistical differences ($p<0.05$) between red alder overstory and unfertilized plots under Douglas-fir overstory ($F_{1,6}$), red alder overstory and fertilized plots under Douglas-fir overstory ($F_{1,6}$), and for comparisons between unfertilized and fertilized plots under Douglas-fir overstory ($F_{1,3}$). Standard error is from four replicates of each overstory or fertilization treatment based on 4 replications of overstory or fertilization treatment.

Table 3.3. Initial chemical composition of senesced leaf litter from 8 Douglas-fir litter sources.

	Percent of Original Litter Material											
	Nutrients					Carbon Compounds				Integrated Measures		
Source Litter	**N**	**P**	**Ca**	**Mg**	**K**	**C**	**ADF[a]**	**Cellulose**	**Lignin[b]**	**Lignin:N**	**C:N**	**LCI[c]**
Douglas-fir 1 (DF 1)	0.68	0.10	1.42	0.08	0.20	51.4	49.4	13.0	35.0	51.8	76.1	0.73
Douglas-fir 2 (DF 2)	0.76	0.07	1.08	0.10	0.15	52.6	50.0	18.9	30.1	39.6	69.3	0.62
Douglas-fir 3 (DF 3)	0.95	0.09	0.81	0.12	0.22	53.3	47.6	18.2	28.9	30.6	56.4	0.62
Douglas-fir 4 (DF 4)	0.97	0.11	0.86	0.11	0.25	52.4	54.7	19.4	34.9	35.8	53.8	0.61
Douglas-fir 5 (DF 5)	0.98	0.10	1.20	0.1	0.20	53.0	48.7	19.2	29.2	29.8	54.1	0.64
Douglas-fir 6 (DF 6)	1.04	0.09	0.91	0.13	0.20	52.5	53.1	18.7	34.0	32.7	50.5	0.60
Douglas-fir 7 (DF 7)	1.21	0.09	0.70	0.12	0.20	53.7	51.5	18.4	33.0	27.2	44.2	0.65
Douglas-fir 8 (DF 8)	1.31	0.09	0.72	0.13	0.15	53.7	56.2	21.3	34.6	26.5	41.1	0.64

Note: [a] Acid-digestible Fiber (ADF) and lignin determined following Goering and van Soest (1970). Ligno-cellulose index (lignin+cellulose/lignin) calculated following Melillo et al. (1989).

Table 3.4. Correlation matrix of initial litter quality measures of Douglas-fir litter sources (n=8).

	C	N	C:N	Lignin	Lignin:N	Cellulose	ADF	LCI	P	K	Ca
N	**0.83***										
C:N	**-0.82**	**-0.98****									
Lignin	-0.32	0.20	-0.13								
Lignin:N	**-0.93****	**-0.88***	**0.92****	0.26							
Cellulose	**0.75**	**0.72**	**-0.76**	-0.18	**-0.84***						
ADF	0.20	0.61	-0.58	**0.74**	-0.30	0.52					
LCI	-0.45	-0.37	0.51	0.29	0.63	**-0.79**	-0.03				
P	-0.26	0.06	-0.13	0.41	0.08	-0.18	0.19	0.22			
K	-0.25	-0.13	-0.01	-0.10	0.06	-0.22	-0.11	-0.10	**0.76**		
Ca	**-0.80**	**-0.82**	**0.84***	-0.07	**0.81**	**-0.72**	-0.52	0.62	0.12	-0.03	
Mg	**0.72**	**0.83**	**-0.86***	0.07	**-0.82**	**0.73**	0.53	-0.69	-0.16	-0.07	**-0.9***

Values are correlation coefficients. Significant correlations (P< 0.05) are indicated in **bold.** **P < 0.001, *P <0.01

Table 3.5. ANOVA for comparisons of decomposition rate (k y^{-1}) from 8 sources of Douglas-fir litter under each treatment model framework (overstory or fertilization comparisons).

Statistical Model	
1. Unfertilized vs. fertilized plots under Douglas-fir Overstory	***k* (y^{-1})**
DF Fertilization ($F_{1,3}$, *p)*	8.68, 0.06
Source ($F_{7,42}$, *p*)	3.37, 0.006
DF Fertilization*Source ($F_{7,42}$, *p*)	1.43, 0.22
2. Red alder Overstory vs. fertilized plots under Douglas-fir Overstory	***k* (y^{-1})**
Added N ($F_{1,6}$, *p)*	2.26, 0.18
Source ($F_{7,42}$, *p*)	5.07, 0.0003
Added N*Source ($F_{7,42}$, *p*)	2.13, 0.06
3. Red alder Overstory vs. unfertilized plots under Douglas-fir Overstory	***k* (y^{-1})**
Site ($F_{1,6}$, *p)*	1.59, 0.25
Source ($F_{7,42}$, *p*)	5.54, 0.0001
Site*Source ($F_{7,42}$, *p*)	1.46, 0.21

Table 3.6. Biomass remaining and decomposition rate (k y^{-1}) of various Douglas-fir litter sources after 2 years in plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory. Standard error calculated for each overstory or fertilization treatment (n=4).

	Biomass Remaining (%)			Decomposition Rate ($k y^{-1}$)		
Source Litter	**Douglas-fir Overstory** (unfertilized plots)	**Douglas-fir Overstory** (fertilized plots)	**Red Alder Overstory**	**Douglas-fir Overstory** (unfertilized plots)	**Douglas-fir Overstory** (fertilized plots)	**Red Alder Overstory**
DF1	55.6 ±0.79	64.8 ±2.88	55.6 ±2.12	0.29 ±.002	0.23 ±0.041	0.27 ±0.019
DF2	59.0 ±2.78	68.5 ±1.79	63.3 ±1.3	0.25 ±0.016	0.19 ±0.018	0.23 ±0.024
DF3	57.8 ±3.12	67.9 ±1.89	63.9 ±4.03	0.26 ±0.011	0.19 ±0.012	0.21 ±0.023
DF4	60.6 ±4.81	68.8 ±2.22	60.0 ±1.66	0.26 ±0.021	0.18 ±0.003	0.24 ±0.016
DF5	52.8 ±2.76	66.1 ±1.45	61.4 ±5.74	0.30 ±0.014	0.20 ±0.009	0.23 ±0.025
DF6	61.8 ±1.51	68.9 ±1.37	55.5 ±2.64	0.25 ±0.004	0.20 ±0.003	0.27 ±0.024
DF7	62.7 ±2.91	67.8 ±3.36	69.0 ±3.25	0.22 ±0.023	0.19 ±0.013	0.18 ±0.031
DF8	60.8 ±1.59	65.2 ±3.36	66.1 ±2.8	0.24 ±0.018	0.20 ±0.021	0.20 ±0.029

Table 3.7. AIC ranking results evaluating the relationship between any one initial litter quality measure and decomposition rate within a single overstory or fertilization treatment (i.e. plots under red alder overstory and unfertilized and fertilized plots under Douglas-fir overstory (n=4).

Overstory or Fertilization Treatment								
Unfertilized plots at Douglas-fir overstory (UDF)			Fertilized plots at Douglas-fir overstory (FDF)			Red Alder Overstory (RA)		
Litter Quality Measure	AIC	Δ AIC	Litter Quality Measure	AIC	Δ AIC	Litter Quality Measure	AIC	Δ AIC
P (+)	**-113.5**	**0**	**LCI (+)**	**-144.9**	**0**	**Ca (+)**	**-117.1**	**0**
N (-)	**-112.4**	**1.1**	**Cellulose (-)**	**-143.7**	**1.2**	**Lignin:N (+)**	**-115.4**	**1.7**
K (+)	**-112.1**	**1.4**	**Lignin:N (+)**	**-141.1**	**3.8**	**N (-)**	**-114.5**	**2.6**
Mg (-)	**-111.7**	**1.8**	Ca (+)	-138.5	6.4	LCI (+)	-110.7	6.4
Ca (+)	**-111.4**	**2.1**	Mg (-)	-137.8	7.1	Cellulose (-)	-110.5	6.6
Lignin:N (+)	**-110.6**	**2.9**	Lignin (+)	-137.5	7.4	Mg (-)	-110	7.1
ADF (-)	**-110.2**	**3.3**	N (-)	-137.2	7.7	*Null Model*	*-109.3*	*7.8*
Cellulose (-)	**-110.1**	**3.4**	P (+)	-136.3	8.6	Lignin (+)	-107.3	9.8
LCI (+)	-108.2	5.3	ADF (-)	-135.8	9.1	P (+)	-106.9	10.2
Lignin (-)	-107.8	5.7	K (+)	-135.5	9.4	K (+)	-106.7	10.4
Null Model	*-100.3*	*13.2*	*Null Model*	*-129.4*	*15.5*	ADF (-)	-106.4	10.7

Note: AIC values are ranked from smallest to largest with smallest value indicating that it is most closely related to decomposition rate. A Δ AIC less than 4 AIC units indicates competing models. Value in parenthesis indicates whether the relationship between the chemical character and decomposition is positive or negative. The null model examines the relationship between decomposition rate and the eight Douglas-fir litter sources without relating this relationship to any initial litter quality factor.

Table 3.8a. Hierarchical linear model results evaluating relationships between initial litter quality and decomposition as influenced by overstory or fertilization treatment.

Statistical Model for HLM Comparisons

1. Douglas-fir (unfertilized and fertilized plots)		2. Red alder and Douglas-fir (fertilized plots)		3. Red alder and Douglas-fir (unfertilized plots)	
UDF vs. FDF	($F_{1,3}$ *p*)	**RA vs. FDF**	($F_{1,6}$ *p*)	**RA vs. UDF**	($F_{1,6}$ *p*)
Ca	**7.29,0.04**	**Ca**	**9.19, 0.02**	**Ca**	**15.72, 0.007**
Fertilization[a]	0.60, 0.47	Fertilization[b]	0.29, 0.62	Overstory	1.82, 0.23
Ca*Fertilization[a]	0.38, 0.56	Ca*Fertilization	2.30, 0.18	Ca*Overstory	1.47, 0.27
K	3.54, 0.11	K	0.37, 0.56	K	2.20, 0.19
Fertilization[a]	0.14, 0.72	Fertilization[b]	0.01, 0.93	Overstory	0.15, 0.71
K*Fertilization[a]	2.81, 0.14	K*Fertilization	0.20, 0.67	K* Overstory	0.47, 0.52
Mg	**5.79, 0.05**	**Mg**	3.73, 0.10	Mg	5.65, 0.60
Fertilization	4.01, 0.09	Fertilization	2.07, 0.20	Overstory	0.08, 0.79
Mg*Fertilization[a]	0.54, 0.49	Mg*Fertilization	0.48, 0.52	Mg* Overstory	0.02, 0.89
N	5.20, 0.06	**N**	**6.06, 0.05**	**N**	**9.75, 0.02**
Fertilization[a]	**7.25, 0.04**	**Fertilization[b]**	**6.69, 0.04**	Overstory	0.02, .91
N*Fertilization[a]	0.81, 0.40	N*Fertilization[b]	1.86, 0.22	N* Overstory	0.40, 0.55
P	**5.71, 0.05**	**P**	1.33, 0.29	P	3.55, 0.11
Fertilization	0.19, 0.68	Fertilization	0.04, 0.86	Overstory	0.29, 0.61
P*Fertilization[a]	1.75, 0.23	P*Fertilization[b]	0.05, 0.84	P* Overstory	0.59, 0.47

Note: [a] - indicates comparison between unfertilized plots and fertilized plots under Douglas-fir overstory [b] - indicates comparison between plots under red alder overstory and fertilized plots under Douglas-fir overstory. Bold indicates significant statistical result from the HLM model.

Table 3.8b. Hierarchical linear model results evaluating relationships between initial litter quality and decomposition as influenced by overstory or fertilization treatment.

Statistical Model for HLM Comparisons

1. Unfertilized and Fertilized Douglas-fir Plots		2. Red alder and Fertilized Douglas-fir Plots		3. Red alder and Douglas-fir Overstory	
UDF vs. FDF	($F_{1,6}$ p)	**RA vs. FDF**	($F_{1,6}$ p)	**RA vs. UDF**	($F_{1,6}$ p)
ADF	2.36, 0.18	ADF	0.30, 0.60	ADF	1.77, 0.23
Fertilization[b]	**1.99, 0.02**	Fertilization[a]	0.04, 0.84	Overstory	0.92, 0.37
ADF*Fertilization	0.90, 0.38	ADF*Fertilization[a]	0.00, 0.99	ADF* Overstory	0.63, 0.46
Cellulose	**5.81, 0.05**	Cellulose	8.47, 0.03	Cellulose	4.18, 0.09
Fertilization[b]	0.52, 0.50	Fertilization[a]	0.73, 0.43	Overstory	0.02, 0.88
Cellulose*Fertilization	0.04, 0.86	Cellulose*Fertilization[a]	0.12, 0.74	Cellulose* Overstory	0.16, 0.70
Lignin	0.06, 0.81	Lignin	2.53, 0.16	Lignin	0.11, 0.75
Fertilization[b]	3.49, 0.11	Fertilization[a]	0.01, 0.91	Overstory	1.58, .26
Lignin*Fertilization	1.97, 0.21	Lignin*Fertilization[a]	0.02, 0.89	Lignin* Overstory	1.49, 0.27
LCI	**6.30, 0.05**	**LCI**	**11.89,0.01**	**LCI**	**4.97, 0.07**
Fertilization[b]	1.52, 0.26	Fertilization[a]	0.01, 0.91	Overstory	1.12, 0.33
LCI*Fertilization	0.88, 0.38	LCI*Fertilization[a]	0.12, 0.74	LCI* Overstory	1.03, 0.35
Lignin:N	**7.68, 0.03**	**Lignin:N**	**8.28, 0.03**	**Lignin:N**	**10.20, 0.02**
Fertilization[b]	1.06, 0.34	Fertilization[a]	0.08, 0.78	Overstory	1.31, 0.30
Lignin:N *Fertilization	0.02, 0.90	Lignin*Fertilization[a]	1.06, 0.34	Lignin:N * Overstory	1.02, 0.35

Note: [a] - indicates comparison between unfertilized plots and fertilized plots under Douglas-fir overstory [b] - indicates comparison between plots under red alder overstory and fertilized plots under Douglas-fir overstory. Bold indicates significant statistical result from the HLM model.

Table 3.9. N dynamics of Douglas-fir litter including initial values and values after 2 years of decomposition. Error represents standard error calculated for each overstory or fertilization treatment (n=4).

Source	Initial N mg/g	Initial C:N	N mg/g	N (mg) Immobilized: gram initial litter	% Initial N	C:N
Unfertilized plots under Douglas-fir overstory (UDF)			Values from litter after 2 years of decomposition			
DF1	6.8	76	18.3 ±2.33	3.43 ±1.37	151 ±20.1	28 ±3.1
DF2	7.6	69	15.9 ±1.04	1.72 ±0.29	123 ±3.9	32 ±2.3
DF3	9.5	56	19.6 ±1.34	1.82 ±0.80	119 ±8.5	26 ±1.4
DF4	9.7	54	17.6 ±0.38	0.88 ±0.63	109 ±6.5	28 ±0.9
DF5	9.8	54	17.7 ±1.12	-0.64 ±1.23	93 ±12.6	29 ±1.6
DF6	10.4	50	18.2 ±1.16	0.79 ±0.44	108 ±4.2	28 ±1.7
DF7	12.2	44	18.0 ±1.11	-0.93 ±0.31	92 ±2.5	28 ±1.8
DF8	13.1	41	17.8 ±.82	-2.24 ±0.62	83 ±4.7	28 ±1.2
Fertilized plots under Douglas-fir overstory (FDF)			Values from litter after 2 years of decomposition			
DF1	6.8	76	16.9 ±0.80	4.23 ±0.93	163 ±13.9	30 ±1.6
DF2	7.6	69	17.1 ±1.00	4.14 ±0.79	155 ±10.4	29 ±1.8
DF3	9.5	56	18.9 ±0.45	3.45 ±0.57	137 ±6.0	27 ±0.6
DF4	9.7	54	18.5 ±0.62	2.95 ±0.61	130 ±6.3	28 ±0.8
DF5	9.8	54	18.1 ±0.73	2.18 ±0.72	122 ±7.4	29 ±1.3
DF6	10.4	50	19.8 ±0.51	3.19 ±0.30	131 ±2.9	26 ±0.4
DF7	12.2	44	22.4 ±0.24	3.06 ±0.92	125 ±7.6	23 ±0.4
DF8	13.1	41	20.5 ±0.96	0.43 ±2.99	103 ±11.5	25 ±1.3
Red alder overstory (RA)			Values from litter after 2 years of decomposition			
DF1	6.8	76	21.7 ±1.63	5.41 ±1.33	180 ±19.8	22 ±1.6
DF2	7.6	69	18.5 ±1.62	4.1±1.13	154 ±14.9	27 ±1.6
DF3	9.5	56	19.0 ±1.60	2.91 ±1.81	131 ±19.2	26 ±2.2
DF4	9.7	54	18.8 ±0.80	1.55 ±0.57	116 ±19.2	26 ±1.7
DF5	9.8	54	20.0 ±1.62	2.5 ±1.40	126 ±14.3	24 ±1.9
DF6	10.4	50	20.2 ±2.42	0.99 ±1.80	110 ±17.2	25 ±3.0
DF7	12.2	44	17.0 ±2.26	-0.32 ±1.79	97 ±14.8	31 ±2.3
DF8	13.1	41	18.8 ±1.83	-0.54 ±1.64	96 ±12.8	27 ±2.3

note: † Negative value indicates net N mineralization. Values over 100% indicate net immbolization and values under 100% indicate mineralization.

Table 3.10. Hierarchical linear model results for tests of the relationship between initial litter percent N of Douglas-fir source and the net N immobilized (mg) per g of initial litter.

Statistical Model

1. Unfertilized and Fertilized Douglas-fir Plots		2. Red alder and Fertilized Douglas-fir Plots		3. Red alder and Douglas-fir Overstory	
UDF vs. FDF	($F_{1,3}$ p)	**RA vs. FDF**	($F_{1,6}$ p)	**RA vs. UDF**	($F_{1,6}$ p)
Initial N	**40.86, 0.0007**	**Initial N**	**31.03, 0.001**	**Initial N**	**42.73, 0.0006**
Fertilization[b]	0.12, 0.74	Fertilization[a]	4.15, 0.09	Overstory	1.70, 0.24
Initial N*Fertilization[a]	2.59, 0.16	Initial N*Fertilization[a]	3.65, 0.10	Initial N*Overstory	0.43, 0.54

Note: [a] - indicates comparison between plots under naturally N rich red alder overstory and fertilized plots under Douglas-fir overstory, [b] - indicates comparison between unfertilized plots and fertilized plots under Douglas-fir overstory, and bold indicates significant statistical result from the HLM model.

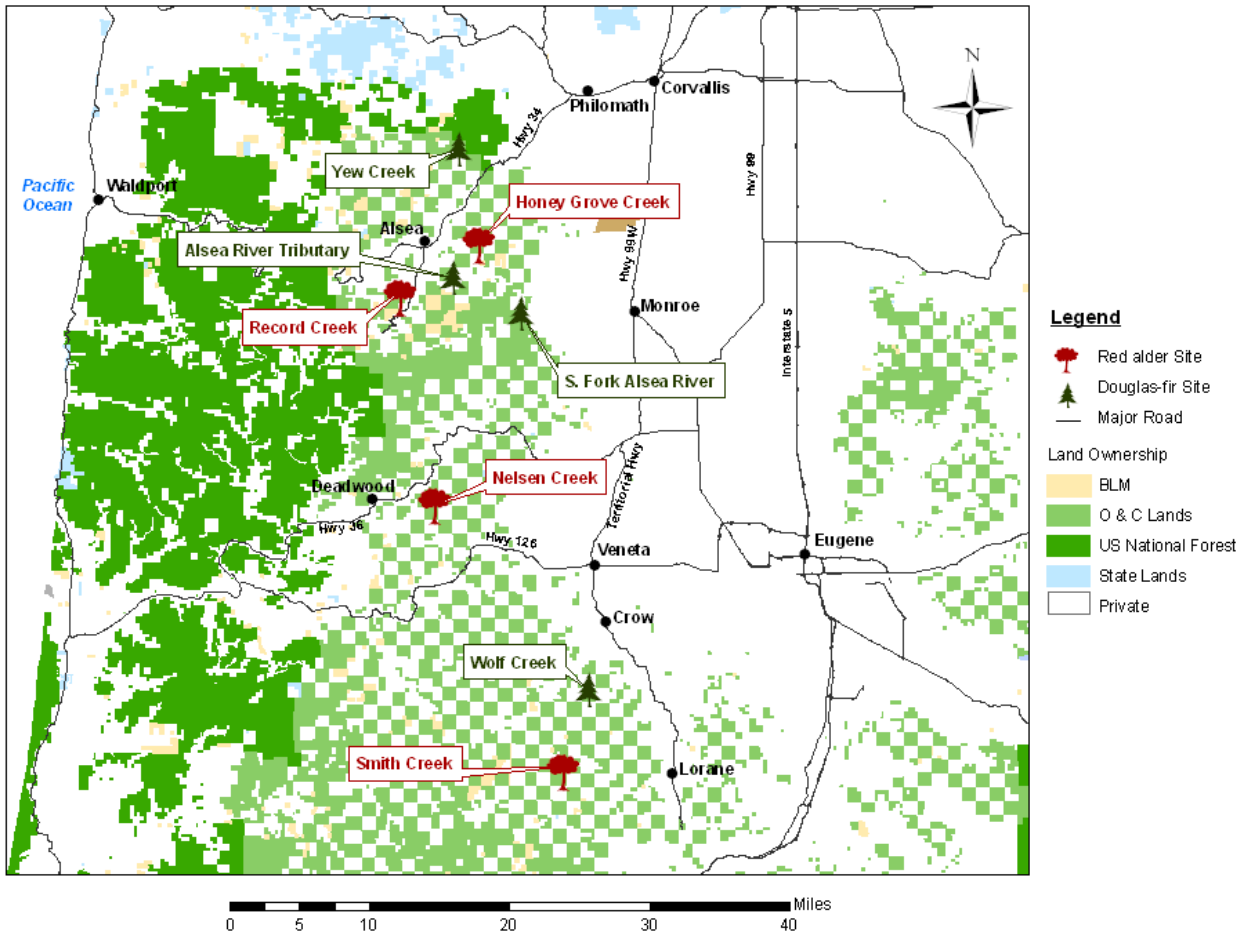

Figure 3.1. Site Map.

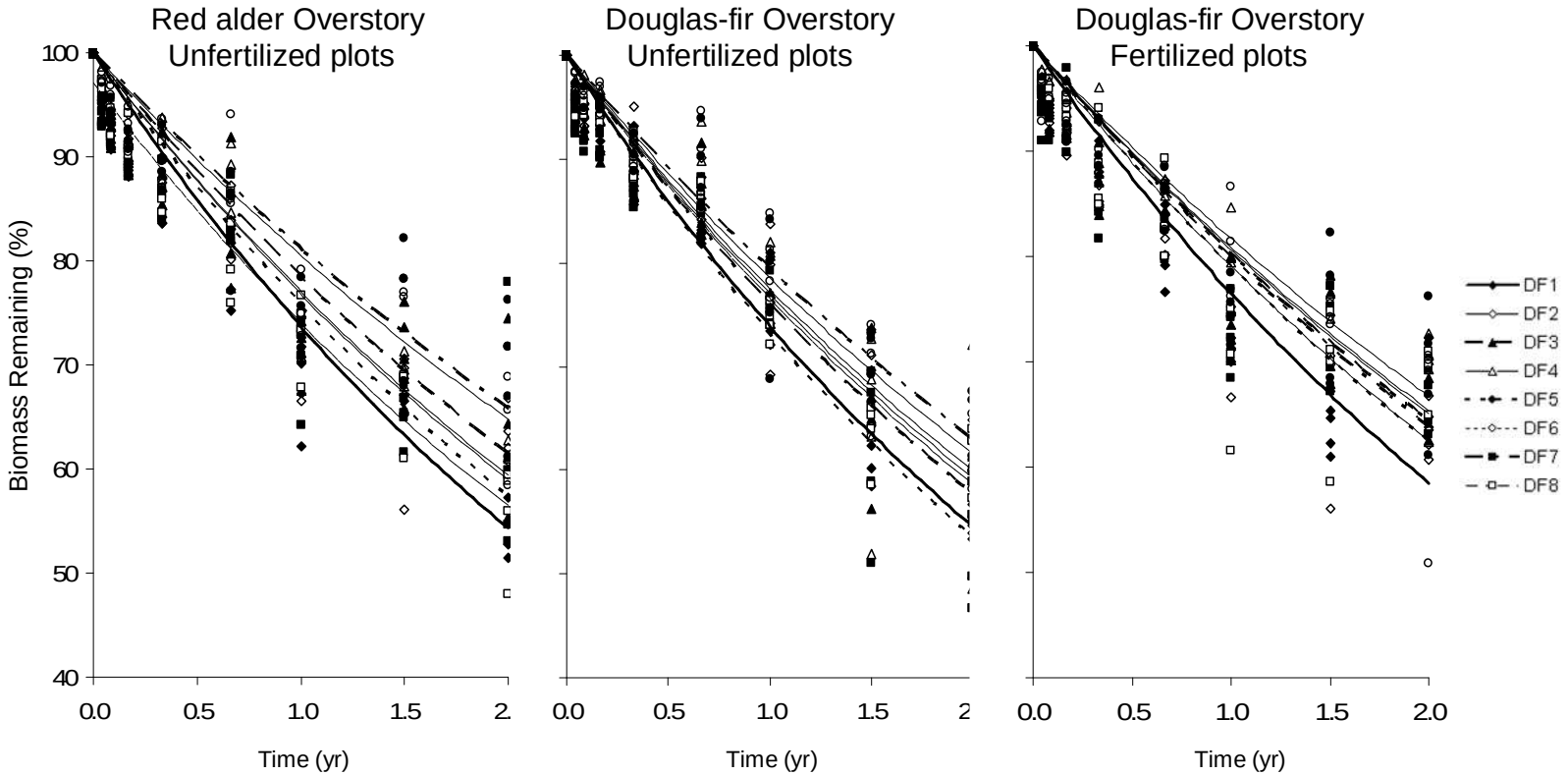

Figure 3.2. Biomass remaining for eight Douglas-fir litter sources from plots under red alder overstory and from unfertilized and fertilized plots under Douglas-fir overstory. Each point represents the average of the 4 overstory or fertilization treatment replications. Error bars represent standard error calculated for each overstory or fertilization treatment (n=4). Bags were placed in field in November 2003 with last collection in November 2005. Regression lines for each litter source from single exponential model.

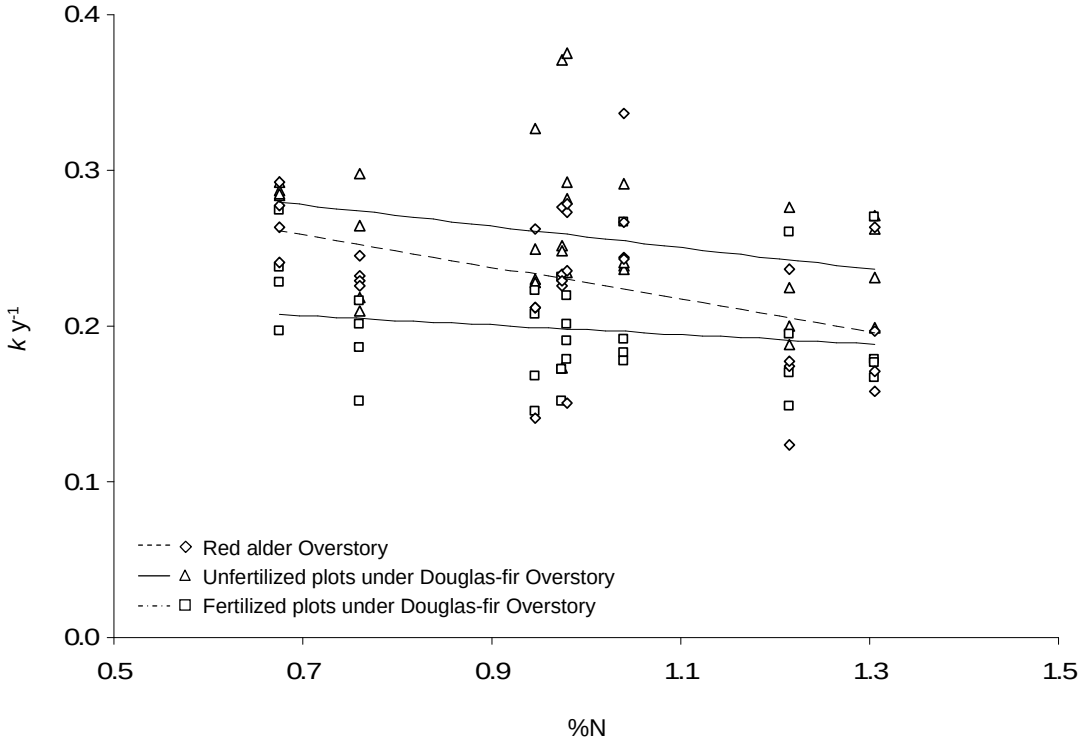

Figure 3.3. Decomposition rate versus initial litter percent N of eight Douglas-fir litter sources from plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory.

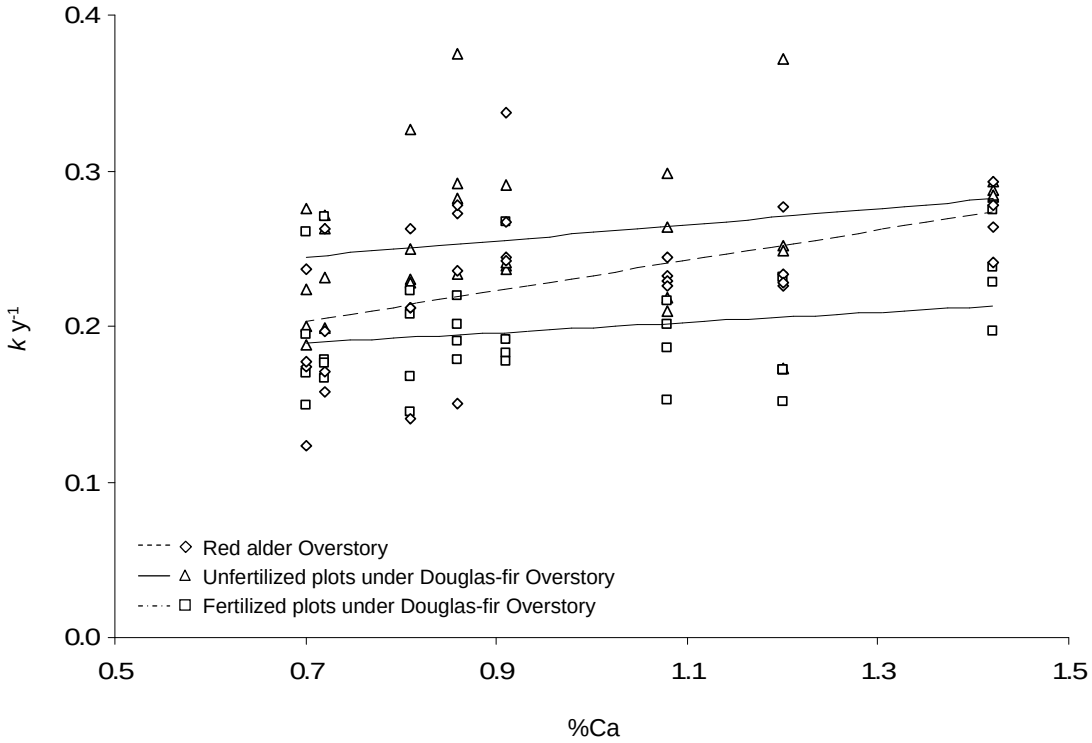

Figure 3.5. Decomposition rate versus initial litter percent Ca of eight Douglas-fir litter sources from plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory.

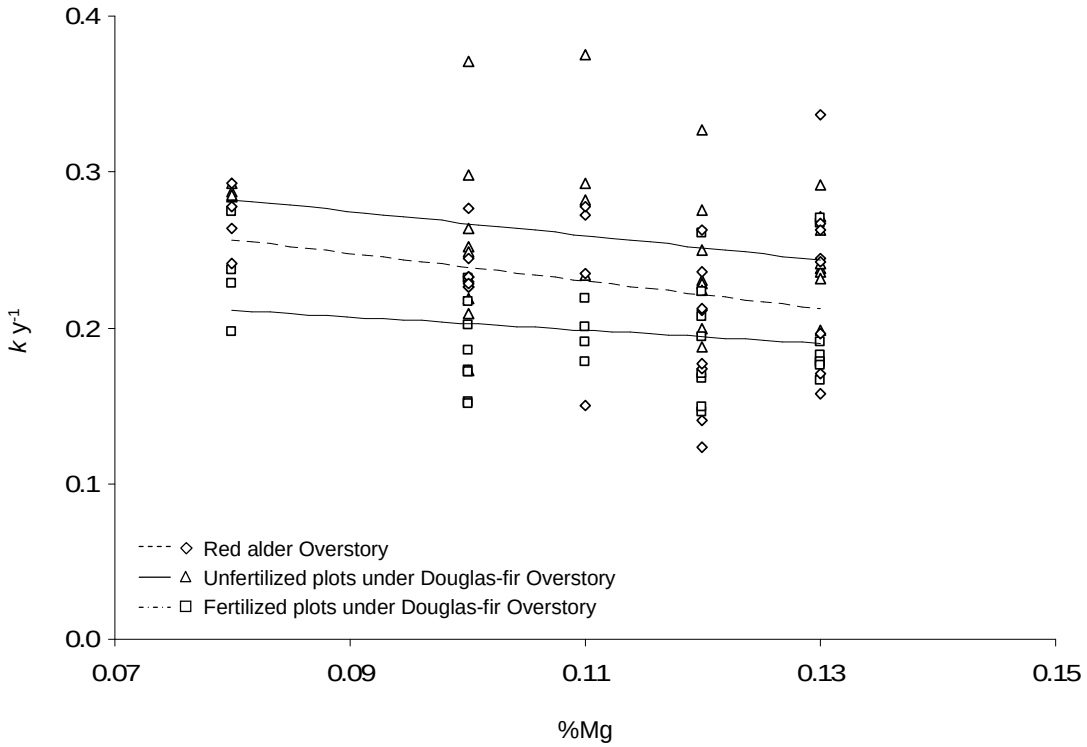

Figure 3.6. Decomposition rate versus initial litter percent Mg of eight Douglas-fir litter sources from plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory.

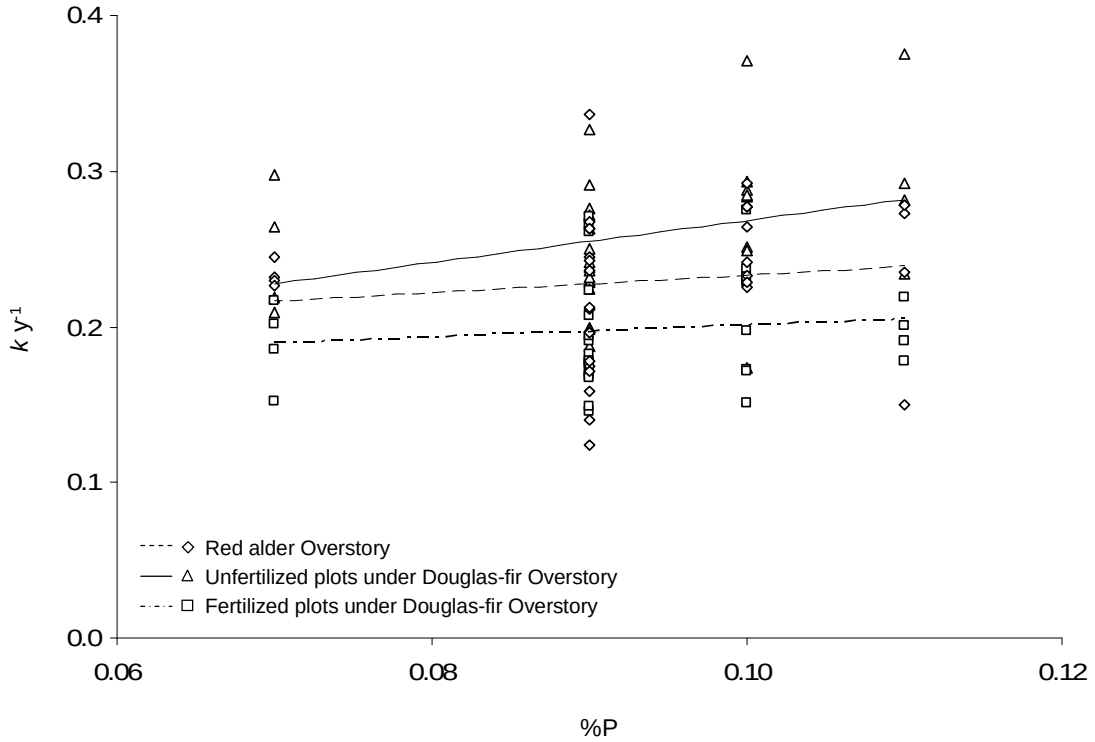

Figure 3.7. Decomposition rate versus initial litter percent P of eight Douglas-fir litter sources from plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory.

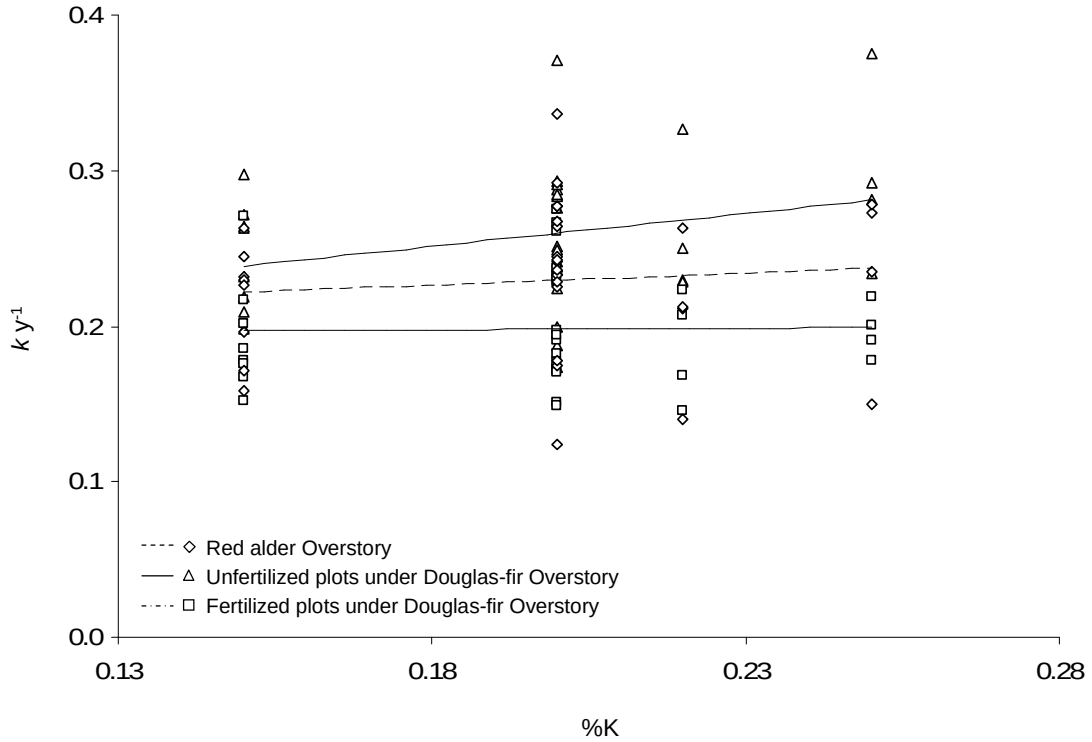

Figure 3.8. Decomposition rate versus initial litter percent K of eight Douglas-fir litter sources from plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory.

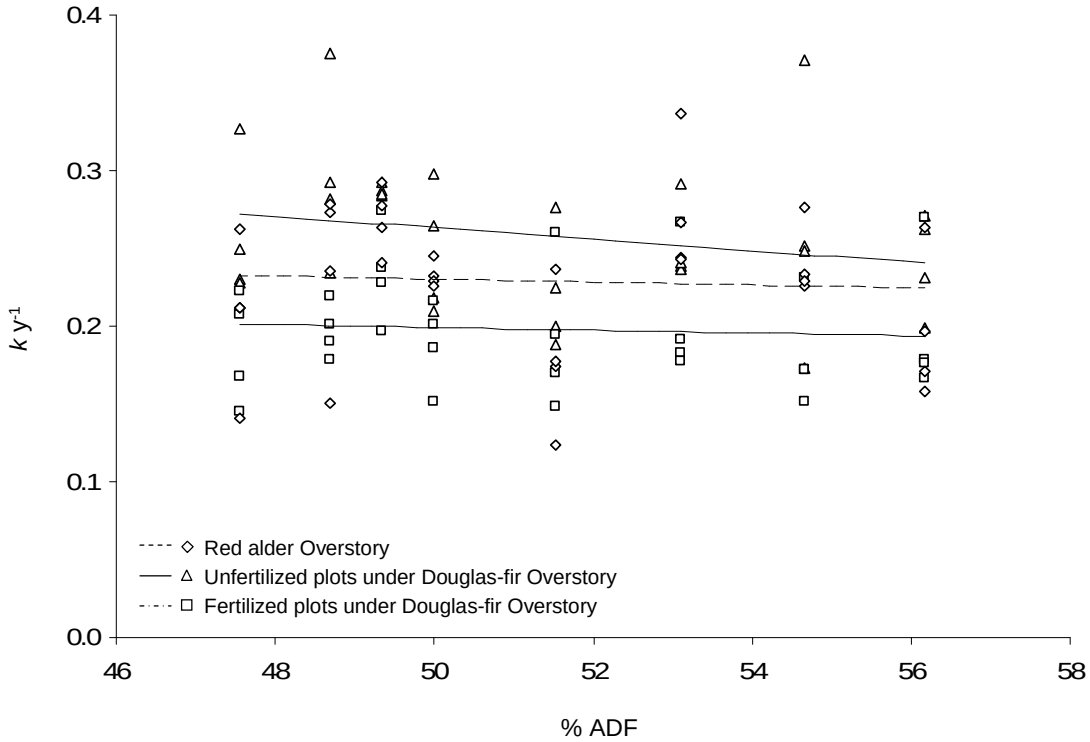

Figure 3.9. Decomposition rate versus initial litter percent ADF of eight Douglas-fir litter sources from plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory.

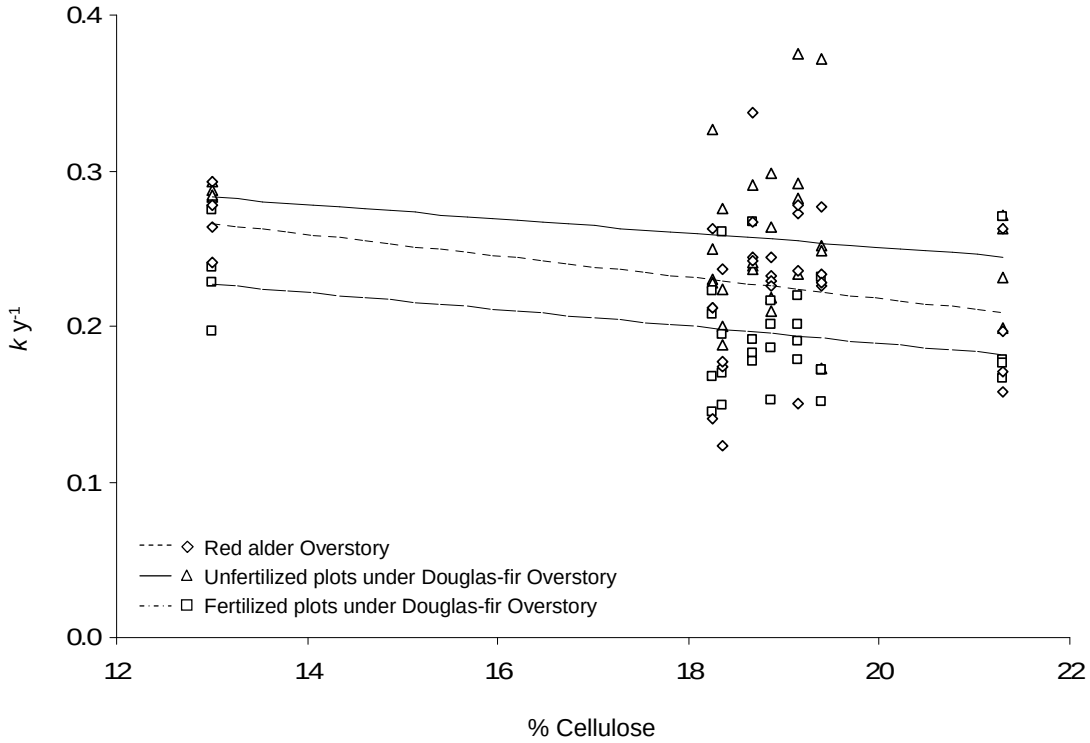

Figure 3.10. Decomposition rate versus initial litter percent cellulose of eight Douglas-fir litter sources in plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory.

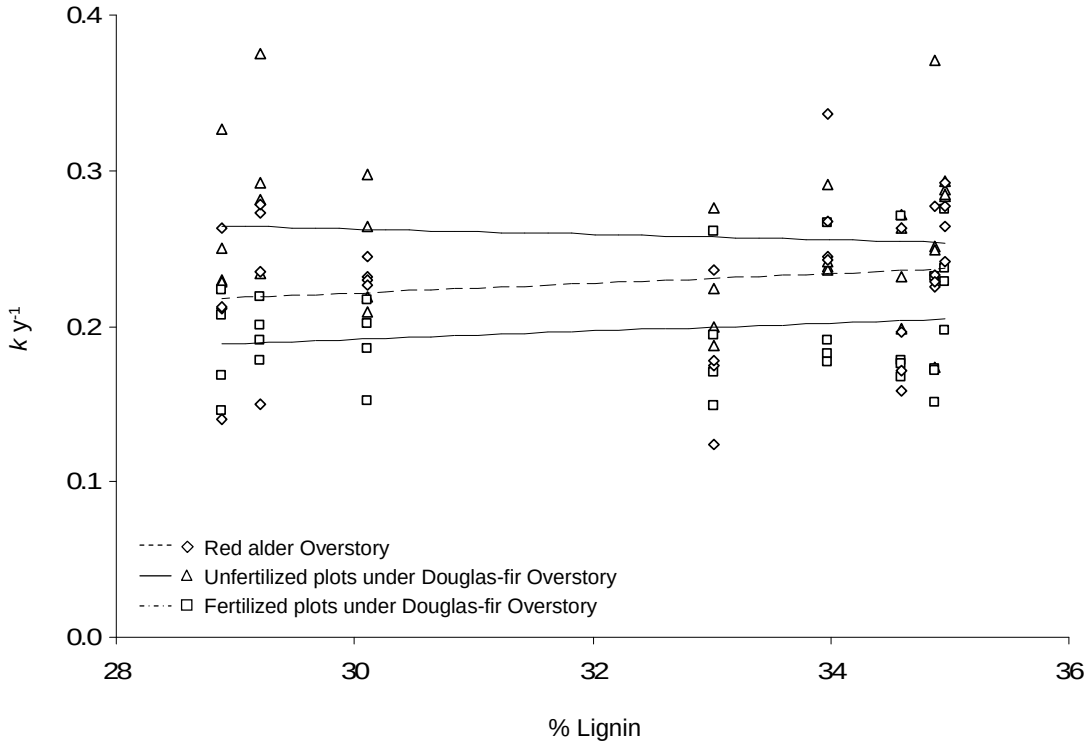

Figure 3.11. Decomposition rate versus initial litter percent lignin of eight Douglas-fir litter sources in plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory.

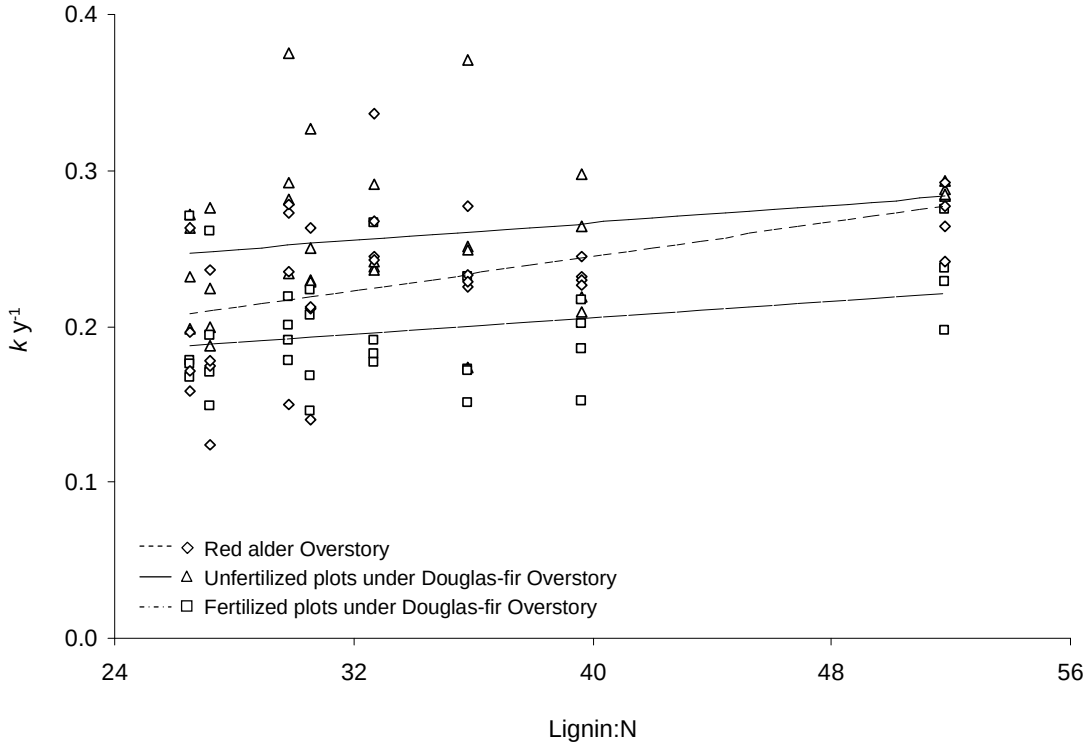

Figure 3.12. Decomposition rate versus initial litter percent lignin:N of eight Douglas-fir litter sources in plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory.

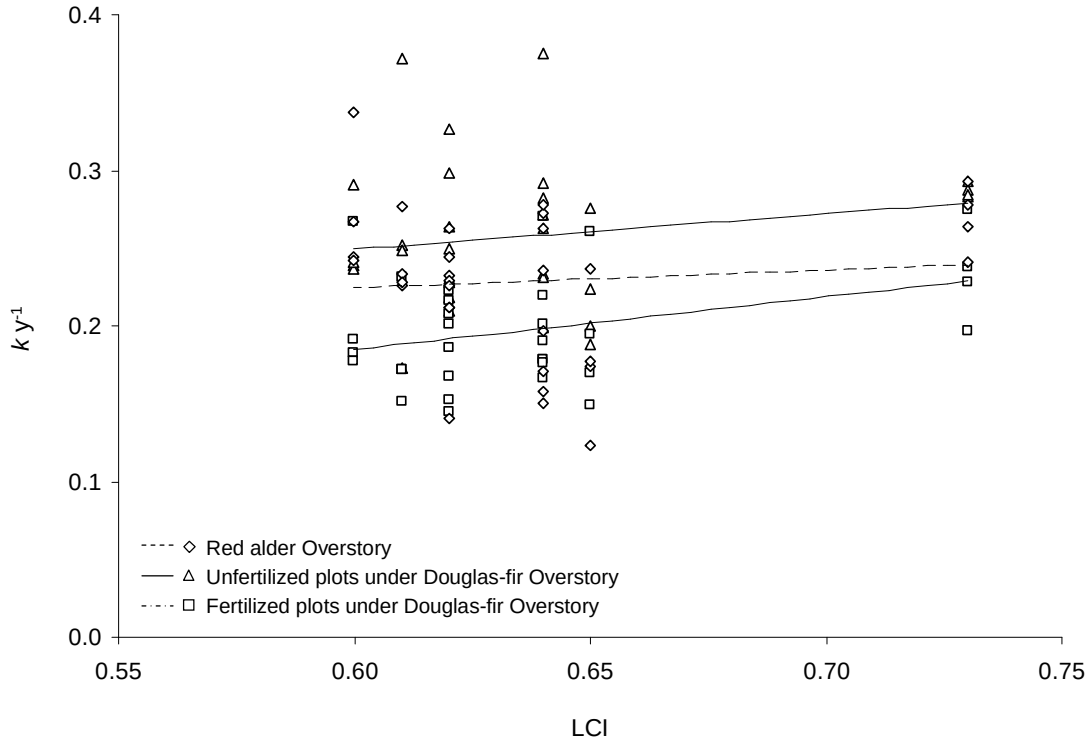

Figure 3.13. Decomposition rate versus initial litter percent LCI of eight Douglas-fir litter sources in plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory

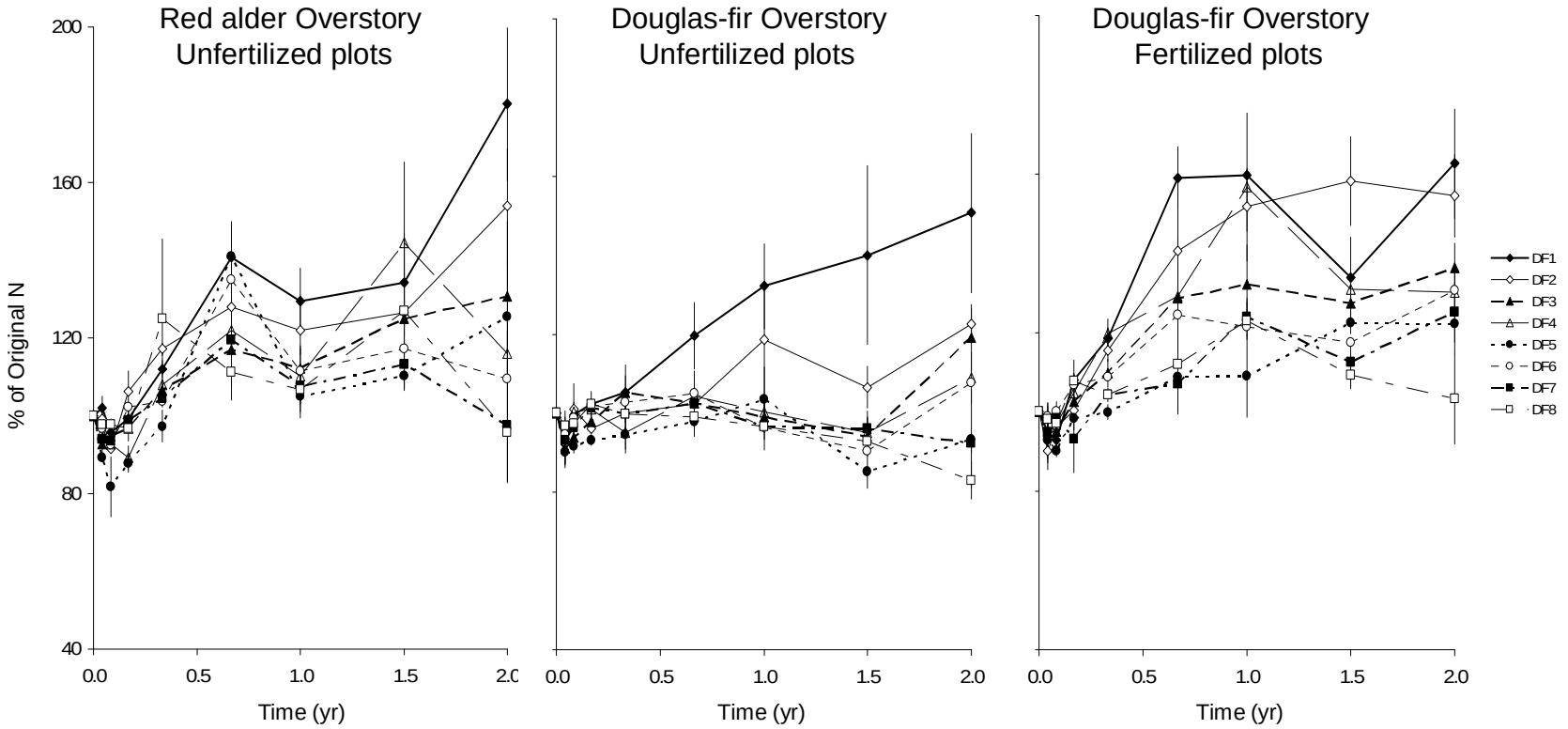

Figure 3.14. Percent of initial N from 8 Douglas-fir litter sources at red alder sites and unfertilized and fertilized plots at Douglas-fir sites. Each point represents the average of the 4 site or fertilization treatment replications. Error bars represent standard error calculated for each overstory or fertilization treatment (n=4). Bags were placed in field in November 2003 with last collection in November 2005.

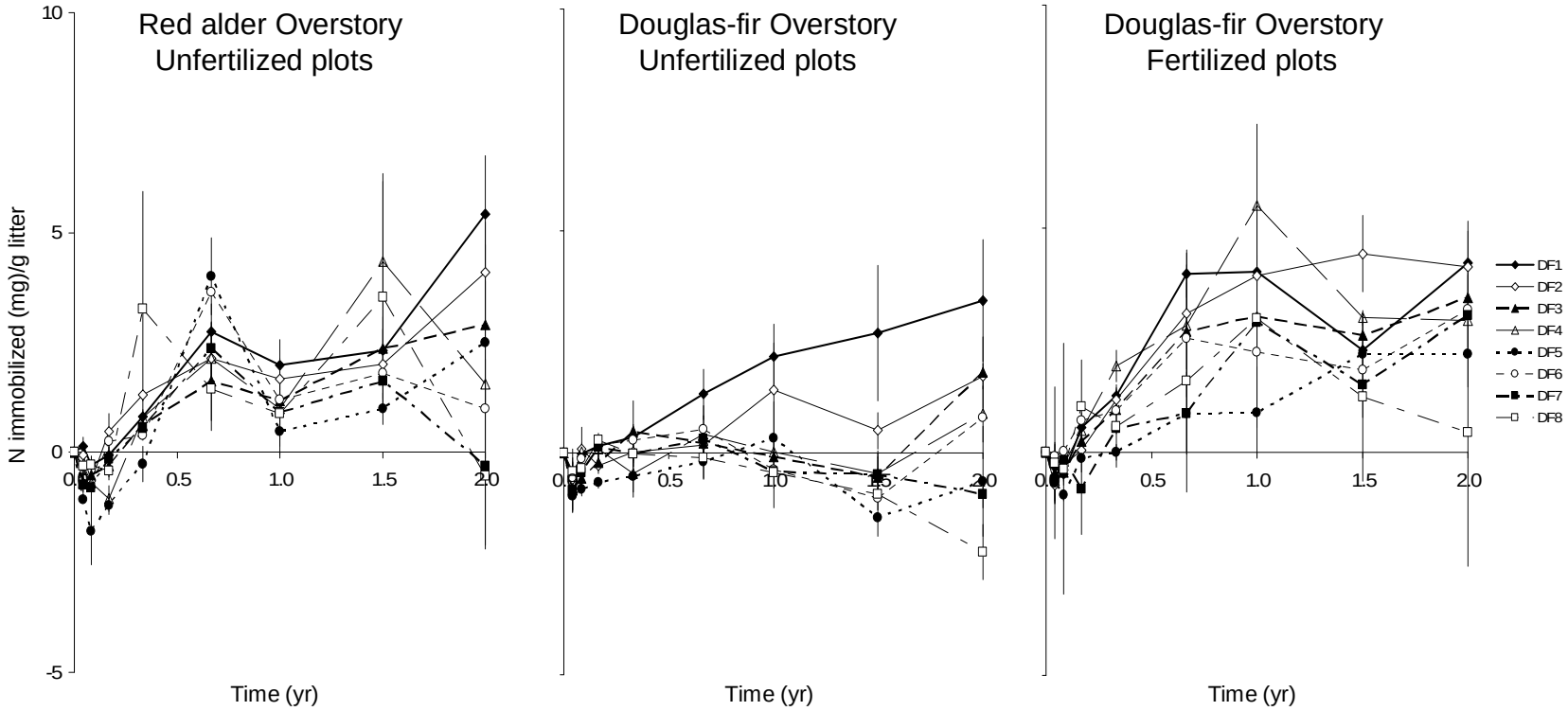

Figure 3.15. Net N immobilized (mg) per gram initial litter from 8 Douglas-fir litter sources at red alder sites and unfertilized and fertilized plots at Douglas-fir sites. Each point represents the average of the 4 site or fertilization treatment replications. Error bars represent standard error calculated for each overstory or fertilization treatment (n=4). Bags were placed in field in November 2003 with last collection in November 2005.

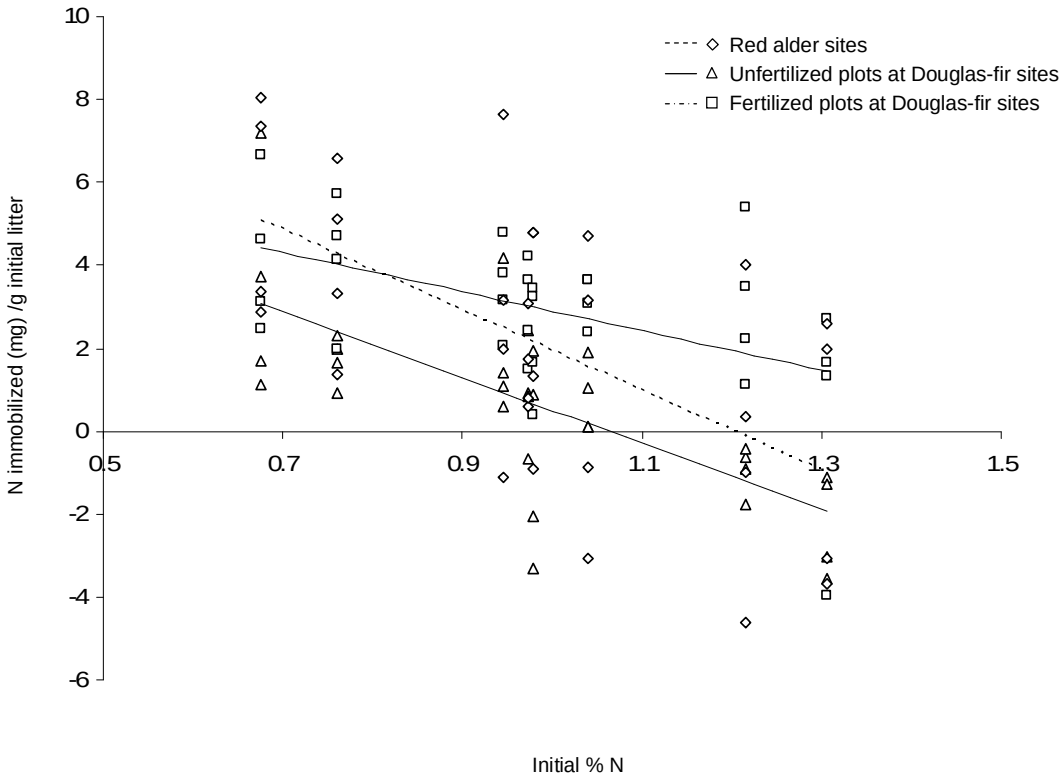

Figure 3.16. Net N immobilized (mg) per gram of initial litter versus initial litter percent N for eight Douglas-fir litter sources in plots under red alder overstory and in unfertilized and fertilized plots under Douglas-fir overstory.

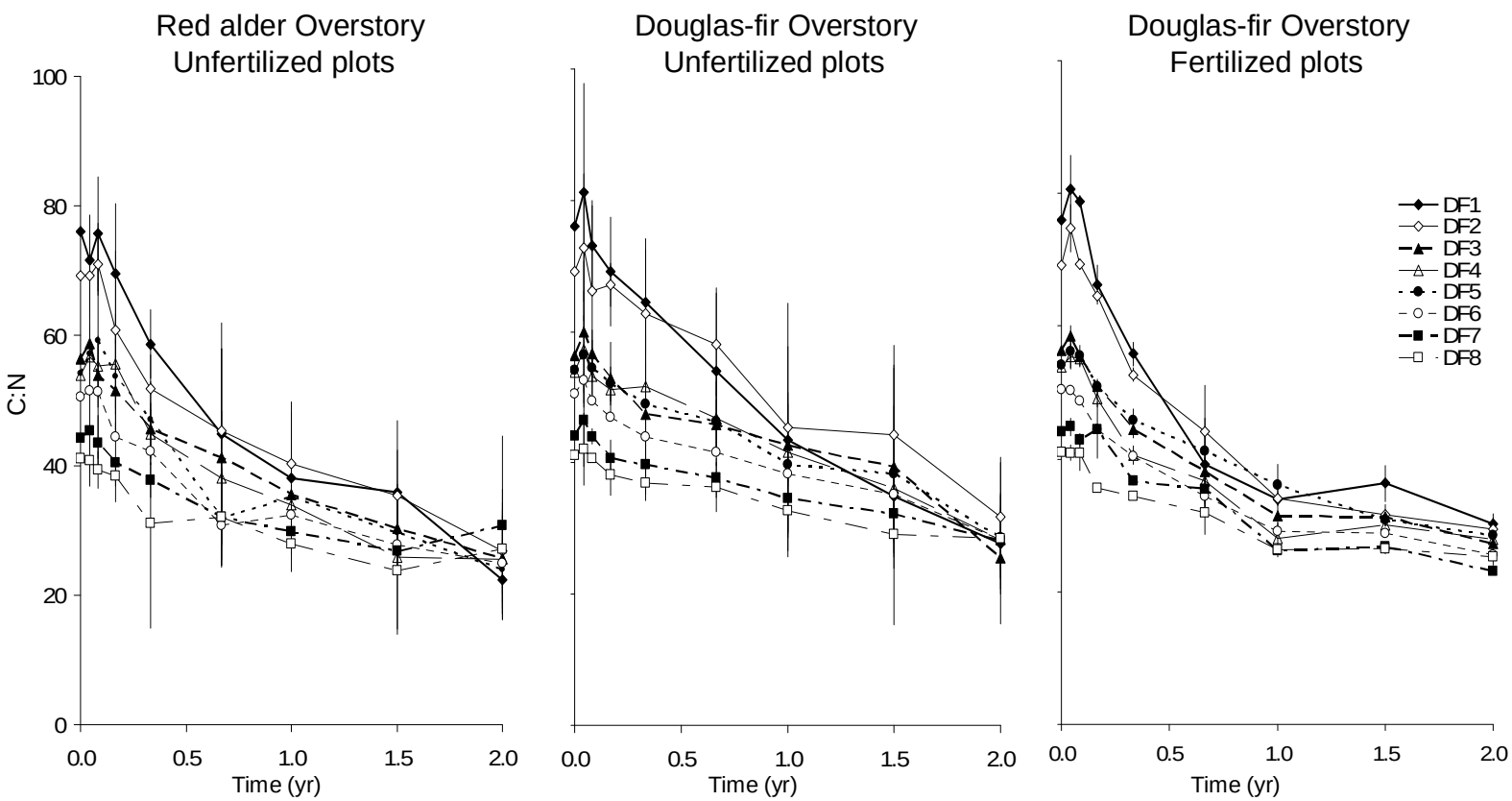

Figure 3.17. C:N ratio of from 8 Douglas-fir litter sources at red alder sites and unfertilized and fertilized plots at Douglas-fir sites. Each point represents the average of the 4 site or fertilization treatment replications. Each point represents the average of the 4 site or fertilization treatment replications. Error bars represent standard error calculated for each overstory or fertilization treatment (n=4). Bags were placed in field in November 2003 with last collection in November 2005.