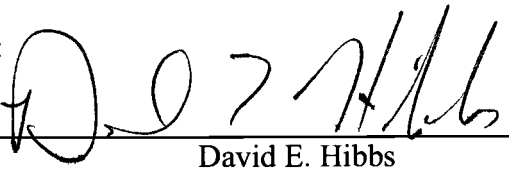
AN ABSTRACT OF THE THESIS OF

Emily E. Scott for the degree of Master of Science in Forest Science presented on March 17, 2004.
Title: The Use of $\delta^{15}N$ and $\delta^{13}C$ to Analyze Food Webs and Identify Source-Sink Relationships in Riparian Canopy Vegetation of the Oregon Coast Range

Abstract approved: 

David E. Hibbs

In the Coast Range of western Oregon, some natural resource managers are converting red alder-dominated riparian areas to conifers to increase the future source of in-stream large wood for salmonid habitat. However, studies in Alaska have shown red alder-dominated riparian areas support greater invertebrate biomass compared to conifer-dominated areas. In addition, red alder can influence the nutrient dynamics of a site with N-rich litter inputs. Thus, these forest conversions have the potential to change riparian food webs and nutrient dynamics.

The objectives of this thesis were to determine the utility of natural abundance stable isotopes of nitrogen and carbon in food web analyses and to describe nutrient dynamics and source-sink relationships in red alder- and Douglas-fir-dominated riparian areas of the central Oregon Coast Range. We address three questions in this study: 1) What is the degree and source of $\delta^{15}N$ and $\delta^{13}C$ variation in foliage of Douglas-fir and red alder? 2) Are Douglas-fir and red alder isotope signatures sufficiently distinct to be used in food web analysis? and 3) Are there differences in nutrient dynamics and source-sink relationships between Douglas-fir- and red alder-dominated riparian areas? To address these questions, we sampled foliage, litterfall, forest floor material, and soil from ten Douglas-fir- and red alder-dominated riparian sites as well as foliage from plantation Douglas-fir and red alder for $\delta^{15}N$, $\delta^{13}C$, and nutrient concentrations.

Douglas-fir had greater variation in foliage $\delta^{15}N$ within a tree crown, within a site, and among sites than red alder. Red alder had consistent foliage $\delta^{15}N$ at all scales, near –1.5‰, a value that is characteristic of nitrogen fixing species. Both species had similar levels of variation in foliage $\delta^{13}C$ at all scales. Douglas-fir was slightly enriched in ^{13}C compared to red alder suggesting greater water-use efficiency in Douglas-fir. Overall, the difference between $\delta^{15}N$ and $\delta^{13}C$ of red alder and Douglas-fir at our study sites were, on average, less than 2.0‰. It is unlikely stable isotopes could be used over broad geographic areas as a tool for determining the contributions of Douglas-fir versus red alder to food webs, although site-specific research may be possible where Douglas-fir and red alder demonstrate greater isotopic differences.

Douglas-fir and red alder exhibited opposite source-sink relationships with soil for N exchange: Douglas-fir was a sink for soil N whereas red alder served as a N source. Douglas-fir sites had a higher N status and lower soil $\delta^{15}N$ along the stream compared to upslope, trends not found at red alder sites. Soil $\delta^{15}N$ near streams on Douglas-fir sites was similar to the soil $\delta^{15}N$ on red alder sites suggesting that a legacy of past red alder along the stream may have contributed to the N status and soil $\delta^{15}N$ gradients on Douglas-fir sites. Soil $\delta^{15}N$ and soil %N did not indicate a presence of marine N on our sites. $\delta^{15}N$ and $\delta^{13}C$ of foliage and soil suggested decomposition processes of leaf litter differed between Douglas-fir and red alder, likely due to different litter chemistries and possible influences on decomposition enzymes. A shift in species composition from red alder-dominated to Douglas-fir-dominated riparian areas would alter source-sink relationships with soil N and litter decomposition processes, although some legacies of soil enrichment in N by red alder would persist.

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The Use of $\delta^{15}N$ and $\delta^{13}C$ to Analyze Food Webs and Identify Source-Sink Relationships in Riparian Canopy Vegetation of the Oregon Coast Range

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

Emily E. Scott, Author

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CONTRIBUTION OF AUTHORS

Dr. Steve Perakis assisted with data interpretation of the second and third chapters of this thesis.

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INTRODUCTION

Riparian vegetation impacts the aquatic ecosystem and the surrounding terrestrial environment through inputs of leaves and large wood (Gregory et al. 1991). These inputs provide food for aquatic organisms (Richardson 1991, Hutchings et al. 1999), supply critical habitat for many salmonids (Reeves et al. 2002), and influence rates of decomposition and nutrient cycling (Prescott et al. 2000). The influence of riparian vegetation on litter inputs and nutrient dynamics differs greatly between hardwood- and conifer-dominated riparian forests (Gregory et al. 1991).

In the Coast Range of western Oregon, red alder (*Alnus rubra*) and Douglas-fir (*Pseudotsuga menziesii*) are the principal dominants of riparian vegetation (Spies et al. 2002). At this time, issues of in-stream structural wood are paramount for creating appropriate fish habitat, leading some natural resource managers to prefer conifers in these stream reaches over red alder (Nierenberg and Hibbs 2000). This has led to managing these areas in favor of large conifers by reducing or removing red alder. The ramifications of converting riparian forest from red alder-dominated to conifer-dominated in the Oregon Coast Range are not complete, but may result in a large change in litter inputs and subsequent changes in riparian food webs and nutrient cycles.

Little is known about the relative use by riparian organisms of red alder- or conifer-dominated systems in the Oregon Coast Range. Studies elsewhere in the Pacific Northwest have shown red alder-dominated riparian areas support greater invertebrate biomass compared to conifer-dominated areas (Allan et al. 2003, Piccolo and Wipfli 2002). Removing or significantly reducing riparian red alder

will decrease an important food source and may have impacts on consumers throughout the food web.

Red alder can also influence the nutrient dynamics of a site (Binkley et al. 1992). In terrestrial habitats, N-rich litter inputs from red alder increase the rate of N-cycling compared to sites with only Douglas-fir (Binkley et al. 1992, Bormann et al. 1994). It is reasonable to consider that the removal or reduction of red alder could alter the nutrient dynamics of the riparian system as well.

Analysis of naturally occurring stable isotopes is becoming a frequently used technique in ecology (see reviews by Adams and Grierson 2001, Dawson et al. 2002, Hobson 1999) and may provide insight into the roles of red alder and Douglas-fir in riparian areas. This technique compares naturally occurring, but less common, isotopes, such as ^{15}N and ^{13}C, with the more abundant forms, ^{14}N and ^{12}C. Different biological and physical processes alter the ratio of the isotopes of an element as a reaction occurs to produce different isotope "signatures" (Peterson and Fry 1987). The resulting isotope signature, or ratio, is compared to that of a standard, usually atmospheric N_2 for N or Pee Dee Belemnite for C, to produce a characteristic isotope signature expressed in per mil units (‰) and written as $\delta^{x}E$ (x = the mass of the heavier isotope, E = the element of interest, e.g. $\delta^{15}N$). Isotope fractionation occurs when the isotope signature changes between a source and a sink. Generally, the lower mass in the light isotope is selected for in reactions because it can move and react faster with the reactants (Högberg 1997). As a reaction occurs, the source generally becomes heavier as more of the light isotope is preferentially removed (Peterson and Fry 1987).

Stable isotopes have been used to track nutrient flows through food webs with varying degrees of success (Ben-David et al. 1997, Cherel et al. 2000, Ponsard and Arditi 2000, Wolf et al. 2000, Post 2002) and may be useful in the Oregon Coast Range for identifying food web relationships in red alder and Douglas-fir riparian areas. Current practices for studying source-consumer relationships (e.g. fecal analysis, gut content analysis, observational information) can be time

consuming, biased in favor of organisms that are easy to identify, and often provide information only of what an animal recently ingested. Isotope analysis of hair, blood, or tissue can overcome some of those biases by providing a measure of assimilated nutrients rather than ingested material (Peterson and Fry 1987), and integrating long- and short-term diets in different tissues (Tieszen et al. 1983). However, there are some limitations with stable isotope analysis that could lead to incorrect conclusions about food sources. The movement of nutrients through subsequent trophic levels can result in fractionation of the isotopes, and so can cloud trophic relationships. For N, successive trophic levels are typically enriched in ^{15}N by 3.4‰ (DeNiro and Epstein 1981, Ponsard and Arditi 2000, Post 2002) although the enrichment can range from 2.0‰ to 5.0‰ (Peterson and Fry 1987, Post 2002). Carbon signatures are more tightly conserved between consumers and sources with a trophic fractionation of <1.0‰ (DeNiro and Epstein 1978, Peterson and Fry 1987, Post 2002). Different levels of fractionation in plant and animal tissue can alter the isotope signature making it difficult to identify the source (Tieszen et al. 1983). Also, varied turnover rates of different animal tissues produce a different isotope signature depending on which tissue is analyzed (Tieszen et al. 1983). These complications make it important to have a good base of knowledge of the system being studied.

For stable isotopes to be used as "tracers" through a food web, the different sources in question (i.e. red alder and Douglas-fir) must have distinct isotope signatures (Dawson et al. 2001). It is likely the nitrogen isotope ($\delta^{15}N$) signatures of red alder and Douglas-fir are distinct due to the different methods by which they acquire N. Red alder is known to fix atmospheric N_2 at high rates (Bormann et al. 1994) and may be less subject to soil $\delta^{15}N$ influences (Peterson and Fry 1987). Nitrogen fixing species generally reflect atmospheric $\delta^{15}N$, which is zero, and usually fall within a limited $\delta^{15}N$ range of -2‰ to 2‰ (Shearer and Kohl 1986, Peterson and Fry 1987, Hobbie 1999a). Fractionation during N_2-fixation is usually minimal (Shearer and Kohl 1986, Högberg 1997). Douglas-fir relies on soil

nitrogen pools which are usually more enriched in ^{15}N than the atmosphere (Shearer and Kohl 1986).

It is not clear how distinct the carbon isotopes ($\delta^{13}C$) of red alder and Douglas-fir may be. Both species use the C_3 photosynthetic pathway, which suggests their $\delta^{13}C$ will be similar (Rounick and Winterbourn 1986). However, isotopic differences between evergreen and deciduous species are common (Garten and Taylor 1992, Marshall and Zhang 1994) and may distinguish Douglas-fir and red alder as well.

In addition to identifying source-consumer relationships in food webs, stable isotopes have been used to describe the rate of nutrient cycling in a system and source-sink relationships of nutrient exchange. Patterns of $\delta^{15}N$ in plants and soils have been related to nitrification and/or mineralization rates (Garten 1993, Garten and Van Miegroet 1994, Koopmans et al. 1997, Emmett et al. 1998), level of mycorrhizal associations (Hobbie at al. 1999a, b, Hobbie at al. 2000, Hobbie and Colpaert 2003), inputs of marine-derived N to riparian ecosystems (Ben-David et al. 1998, Helfield and Naiman 2002, Bilby et al. 2003, Reimchen et al. 2003), and the depth and form of N uptake (McKane et al. 2002). Some of the uses of stable isotopes of carbon, $\delta^{13}C$, are to track changes in vegetation composition for species using different photosynthetic pathways (Wedin et al. 1995) and to better understand litter decomposition (Wedin et al. 1995, Quideau et al. 2003) and soil organic matter turnover (Chen et al. 2002).

The Cooperative Forest Ecosystem Research program (CFER, www.fsl.orst.edu/cfer/) created the Analysis of Riparian Management and Aquatic Conservation Strategies (ARMACS) project to address the issue of red alder-conifer conversions in riparian areas of the Oregon Coast Range. Several projects were designed to quantify how certain species of birds, bats, salamanders, some aquatic emergent invertebrates, and spiders respond to varied levels of red alder and Douglas-fir in a stream reach. Also addressed by ARMACS was the feasibility of using natural abundance stable isotopes to evaluate the importance of the

dominant overstory species to food chains and to better understand nutrient dynamics in red alder- versus Douglas-fir-dominated riparian areas. This stable isotope objective is the focus of this thesis. We address three questions in this study: 1) What is the level and source of $\delta^{15}N$ and $\delta^{13}C$ variation in foliage of Douglas-fir and red alder? 2) Are Douglas-fir and red alder isotope signatures sufficiently distinct to be used in food web analysis? and 3) Are there differences in nutrient dynamics and source-sink relationships between Douglas-fir- and red alder-dominated riparian areas? The results of this study will determine whether or not stable isotopes are an appropriate tool for food web analysis in this system. Our results will also identify some potential consequences of converting red alder-dominated areas to those dominated by conifers on the nutrient dynamics of these riparian areas.

References

Adams, M.A., and P.F. Grierson. 2001. Stable isotopes at natural abundance in terrestrial plant ecology and ecophysiology: an update. Plant biology 3: 299-310.

Allan, J.D., M.S. Wipfli, J.P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences 60: 309-320.

Ben-David, M., R.W. Flynn, and D.M. Schell. 1997. Annual and seasonal changes in diets of martens; evidence from stable isotope analysis. Oecologia 111: 280-291.

Ben-David, M., T.A. Hanley, and D.M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. Oikos 83: 47-55.

Bilby, R.E., E.W. Beach, B.R. Fransen, J.K. Walter, and P.A. Bisson. 2003. Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. Transactions of American Fisheries Society 132: 733-745.

Binkely, D., P. Sollins, R. Bell, D. Sachs, and D. Myrold. 1992. Biogeochemistry of adjacent conifer and alder-conifer stands. Ecology 73: 2022-2033.

Bormann, B.T., K. Cormack, Jr., and W.O. Russell III.1994. Influences of red alder on soils and long-term ecosystem productivity. Pages 47-56 *in* D.E. Hibbs, D.S. DeBell, and R.F. Tarrant, editors. The biology and management of red alder. Oregon State University Press, Corvallis, OR.

Cherel, Y., K.A. Hobson, H. Weimerskirch. 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122: 155-162.

Chen, Q., C. Shen, S. Peng, Y. Sun, W. Ui, Z. Li, and M. Jiang. 2002. Soil organic matter turnover in the subtropical mountainous region of south China. Soil Science 167: 401-415.

Dawson, T.E., S. Mambelli, A.H. Planboeck, P.H. Templer, and K.P. Tu. 2002. Stable isotopes in plant ecology. Annual Review of Ecology and Systematics 33: 507-559.

DeNiro, M.J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42: 495-506.

DeNiro, M.J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45: 341-351.

Emmett, B.A., O.J. Kjønaas, P. Gundersen, C. Koopmans, A. Tietema, and D. Sleep. 1998. Natural abundance of 15N in forests across a nitrogen deposition gradient. Forest Ecology and Management 101: 9-18.

Garten, Jr., C.T. 1993. Variation in foliage ^{15}N abundance and the availability of soil nitrogen on Walker Branch Watershed. Ecology 74: 2098-2113.

Garten, Jr., C.T., and G.E. Taylor, Jr. 1992. Foliage $\delta^{13}C$ within a temperate deciduous forest: spatial, temporal, and species sources of variation. Oecologia 90: 1-7.

Garten, Jr., C.T., and H. Van Miegroet. 1994. Relationships between soil nitrogen dynamics and natural ^{15}N abundance in plant foliage from Great Smoky Mountains National Park. Canadian Journal of Forest Research 24: 1636-1645.

Gregory, S.V., F. J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. Focus on links between land and water. Bioscience 8: 540-551.

Helfield, J.M., and R.J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology 82: 2403-2409.

Hobbie, E.A., and J. V. Colpaert. 2003. Nitrogen availability and colonization by mycorrhizal fungi correlate with nitrogen isotope patterns in plants. New Phytologist 157: 115-126.

Hobbie, E.A., S.A. Macko, and H.H. Shugart. 1999a. Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. Oecologia 118: 353-360.

Hobbie, E.A., S.A. Macko, and H.H. Shugart. 1999b. Interpretation of nitrogen isotope signatures using the NIFTE model. Oecologia 120: 405-415.

Hobbie, E.A., S.A. Macko, and M. Williams. 2000. Correlations between foliage $\delta^{15}N$ and nitrogen concentrations may indicate plant-mycorrhizal interactions. Oecologia 122: 273-283.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120: 314-326.

Högberg, P. 1997. Tansley Review No. 95. ^{15}N natural abundance in soil-plant systems. New Phytology 137: 179-203.

Hutchings, M.J., E.A. John, and A.J.A. Stewart (editors). 1999. The Ecological Consequences of Environmental Heterogeneity. The 40th Symposium of the British Ecological Society, University of Sussex.

Koopmans, C.J., D. van Dam, A. Tietema, and J.M. Verstraten. 1997. Natural ^{15}N abundance in two nitrogen saturated forest ecosystems. Oecologia 111: 470-480.

Marshall, J.D., and J. Zhang. 1994. Carbon isotope discrimination and water-use efficiency in native plants of the north-central Rockies. Ecology 75: 1887-1895.

McKane, R.B., L.C. Johnson, G.R. Shaver, K.J. Nadelhoffer, E.B. Rastetter, B. Fry, A.E. Giblin, K. Kielland, B.L. Kwiatkowski, J.A. Laundre, and G. Murray. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415: 68-71.

Nierenberg, T.R., and D.E. Hibbs, 1999. A characterization of unmanaged riparian areas in the central Coast Range of western Oregon. Forest Ecology and Management 129: 195-206.

Peterson, B.J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecological Systems 18: 293-320.

Piccolo, J.J., and M.S. Wipfli. 2002. Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export from headwater streams to downstream habitats in southeastern Alaska? Canadian Journal of Fisheries and Aquatic Sciences 59: 503-513.

Ponsard, S., and R. Arditi. 2000. What can stable isotopes (d15N and $\delta^{13}C$) tell about the food web of soil macro-intertebrates? Ecology 81: 852-864.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703-718.

Prescott, E.C., L.M. Zabek, C.L. Staley, and R. Kabzems. 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. Canadian Journal of Forest Research 30: 1742-1750.

Quideau, S.A., R.C. Graham, X. Feng, and O.A. Chadwick. 2003. Natural isotopic distribution in soil surface horizons differentiated by vegetation. Soil Science Society of America Journal 67: 1544-1550.

Reeves, G.H., K.M. Burnett, and S.V. Gregory. 2002. Fish and aquatic ecosystems of the Oregon Coast Range. Pages 68-98 *in* S.D. Hobbs, J.P. Hayes, R.L. Johnson, G.H. Reeves, T.A. Spies, J.C. Tappeiner, and G.E. Wells, editors. Forest and Stream Management in the Oregon Coast Range. Oregon State University Press, Corvallis, OR.

Reimchen, T.E., D.D. Mathewson, M.D. Hocking, J. Moran, and D. Harris. 2003. Isotopic evidence for enrichment of salmon-derived nutrients in vegetation, soil and insects in riparian zones in Coastal British Columbia. American Fisheries Society Symposium 34: 59-69.

Richardson, J.S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology 72: 873-887.

Rounick, J.S. and M.J. Winterbourn. 1986. Stable carbon isotopes and carbon flow in ecosystems. BioScience 36: 171-177.

Shearer, G., and D.H. Kohl. 1986. N_2-fixation in field settings: estimations based on natural ^{15}N abundance. Australian Journal of Plant. Physiology 13: 699-756.

Spies, T.A., D.E. Hibbs, J.L. Ohmann, G.H. Reeves, R.J. Pabst, F.J. Swanson, C. Whitlock, J.A. Jones, B.C. Wemple, L.A. Parendes, and B.A. Schrader. 2002. The ecological basis of forest ecosystem management in the Oregon Coast Range. Pages 31-67 *in* S.D. Hobbs, J.P. Hayes, R.L. Johnson, G.H. Reeves, T.A. Spies, J.C. Tappeiner, and G.E. Wells, editors. Forest and Stream Management in the Oregon Coast Range. Oregon State University Press, Corvallis, OR.

Tieszen, L.L., T.W. Boutton, K.G. Tesdahl, and N.A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia 57: 32-37.

Wedin, D.A., L.L. Tieszen, B. Dewey, and J. Pastor. 1995. Carbon isotope dynamics during grass decomposition and soil organic matter formation. Ecology 76: 1383-1392.

Wolf, B.O., C. Martinez del Rio. 2000. Use of saguaro fruit by white-winged doves: isotopic evidence of a tight ecological association. Oecologia 124: 536-543.

STABLE ISOTOPE VARIATION IN RIPARIAN VEGETATION OF THE OREGON COAST RANGE

Abstract

Natural abundance stable isotopes have the potential to be a useful tool in food web analyses provided the different food sources being considered are isotopically distinct. In the central Coast Range of Oregon, identifying riparian food webs based on red alder versus Douglas-fir by using stable isotopes is of interest as some managers consider hardwood-to-conifer forest conversions to encourage large wood recruitment to streams for anadromous fish habitat. We analyzed foliage $\delta^{15}N$ and $\delta^{13}C$ from red alder and Douglas-fir at ten riparian sites and a plantation in the Oregon Coast Range to determine the variation in isotope values within a tree crown, within a site, and among sites. Within a tree crown, the $\delta^{15}N$ of Douglas-fir needles varied by on average 2.0‰ in first-year needles from the bottom to the top of the crown and by 0.24‰ among first to third year needles. Red alder had no significant differences in $\delta^{15}N$ within the crown. Red alder $\delta^{13}C$ was more variable with height compared to Douglas-fir (2.12‰ average difference in red alder; 1.01‰ average difference for Douglas-fir). Neither species demonstrated significant differences in $\delta^{13}C$ along a branch into the crown interior. In riparian areas, there was generally greater variation within a site in $\delta^{15}N$ for Douglas-fir (maximum site variation 2.58‰) compared to red alder (0.59‰). $\delta^{13}C$ variation within a site was roughly 3.3‰ for both red alder and Douglas-fir. Across sites, the average variation in $\delta^{15}N$ was greater for Douglas-fir (1.72‰) compared to red alder (0.27‰) while $\delta^{13}C$ variation across sites was similar for both species. The difference between the $\delta^{15}N$ and $\delta^{13}C$ signatures of red alder and Douglas-fir at our study sites were, on average, less than 2.0‰, so it is unlikely stable isotopes could be broadly used as an effective tool for determining the contributions of Douglas-fir versus red alder to food webs in this system.

However, it may be possible to conduct site-specific research where the mean isotope composition of Douglas-fir and red alder are distinct.

Introduction

Understanding food webs in an ecosystem can provide insights into the nature and complexity of species interactions. Unfortunately, because food webs are complex, capturing relationships among organisms can be difficult. Conventional methods for food web studies have relied on observational data as well as gut and fecal content analyses, which are subject to certain biases that can strongly influence conclusions about an organism's food source (DeNiro and Epstein 1978). Gut and fecal content analyses can overestimate the importance of food sources that are poorly digested and easier to identify (McIlwee and Johnson 1998, Herrera et al. 2001). Personal observations of feeding habits are limited by the ability of the observer to clearly see and identify what is being consumed. These methods provide only a snapshot in time of an organism's diet and do not necessarily indicate whether ingested items were assimilated into the tissues of the organism.

Naturally occurring stable isotopes have the potential to mitigate some of these limitations and augment conventional methods. Stable isotope analysis of food webs compares the heavy to light isotope ratio of a consumer ($^{15}N/^{14}N$ or $^{13}C/^{12}C$) with that of its diet (Peterson and Fry 1987). The more similar the isotope signatures are between consumer and source (after accounting for the fractionation of the isotope signature between trophic levels), the greater the relative importance of that food source to the consumer's diet (DeNiro and Epstein 1978, Phillips 2001). Stable isotopes also integrate long-term and short-term diets in tissues with different turnover times (Tieszen et al. 1983) and supply information from organisms that are difficult to observe (Cherel et al. 2000, Polischuk et al. 2001). Other studies have used stable isotopes to follow nutrient flows through parts of

food webs with varying degrees of success (Ben-David et al. 1997, Cherel et al. 2000, Ponsard and Arditi 2000, Wolf and Martinez del Rio 2000, Post 2002).

In the Coast Range of western Oregon, there is great interest in understanding food web relationships in riparian areas dominated by either red alder (*Alnus rubra*) or Douglas-fir (*Pseudotsuga menziesii*). Some riparian areas are being actively managed for the production of large conifers to supply streams with large wood for salmonid habitat at the expense of red alder in the riparian zone (Nierenberg and Hibbs 2000). The impacts of the conversion from a red alder-dominated overstory to one dominated by conifers are incomplete, but it is possible the shift will strongly affect aquatic and terrestrial food webs. Riparian vegetation can significantly contribute to the nutritional resources of both stream and forest food chains (Gregory et al. 1991) either directly through leaf litter or indirectly by providing food and habitat to other organisms (McComb 1994). Red alder-dominated riparian areas can support greater invertebrate mass than areas dominated by conifers (Allan et al. 2003) and may supply fish with more terrestrial prey (Wipfli 1997). The removal of red alder from riparian zones in favor of Douglas-fir and other conifers may decrease some of the benefits of the overstory conversions.

Natural abundance stable isotopes of nitrogen and carbon may serve as "tracers" through food webs in red alder- and Douglas-fir-dominated riparian areas to determine the contribution of each species to aquatic and terrestrial food webs. Dawson et al. (2002) stated, "[u]sing natural abundance isotopes as tracers requires that the different potential sources have repeatable and distinct δ values that are broader than the natural range of plant δ values measured." The $\delta^{15}N$ signature of red alder may differ systematically from Douglas-fir due to alder's ability to fix atmospheric nitrogen. Nitrogen fixers tend to have $\delta^{15}N$ signatures similar to that of the atmosphere, near zero (Shearer and Kohl 1986). Douglas-fir relies on soil nitrogen pools which are usually more enriched in ^{15}N than the atmosphere (Shearer and Kohl 1986). $\delta^{13}C$ is frequently used to distinguish between plants

using different photosynthetic pathways (Rounick and Winterbourn 1986), as well as plants with different water-use efficiencies (Farquhar et al. 1982). It is not clear how distinct the $\delta^{13}C$ of red alder and Douglas-fir will be since both use the C_3 photosynthetic pathway, but isotopic differences between evergreen and deciduous species have been found (Garten and Taylor 1992, Marshall and Zhang 1994) and may allow for the separation of Douglas-fir and red alder isotopically.

The objective of this study was to explore the variation in nitrogen and carbon isotope signatures of Douglas-fir and red alder foliage to evaluate their applicability for use in food web analyses. To do this, we addressed potential isotope variability at several scales: within the tree crown, among trees on a common site, and among sites. We evaluated isotope variations within tree crowns at a red alder and Douglas-fir plantation containing young trees that could be easily, and accurately, sampled at different crown positions. Within-site variability was addressed at the plantation, as well as at ten riparian sites throughout the Oregon Coast Range where we also examined isotope variation across sites. This information then allowed us to address whether natural abundance stable isotopes are a feasible tool for food web analysis in red alder- and Douglas-fir-dominated riparian areas of the Oregon Coast Range.

Methods

Study area

The study area was located in the central Coast Range of Oregon (44° 17'N, 123° 30'W) in the Upper Alsea, Lake Creek, and Lower Siuslaw watersheds. The Coast Range was formed from the uplifted ocean floor during the tertiary period and is composed primarily of marine sandstones, shales, and basaltic volcanic rock (Orr et al. 1992). Soils are generally moderately deep sandy loams to clay loams with dark surface horizons high in organic matter (Franklin and Dyrness 1988). The maritime climate is moderate with warm dry summers and cool wet winters. Rain is the predominant form of precipitation and falls from October to March with

average yearly rainfall of 150 to 300 cm. The study area falls in the western hemlock (*Tsuga heterophylla*) vegetation zone with major forest tree species of Douglas-fir (*Pseudotsuga menziesii*), western hemlock, and western redcedar (*Thuja plicata*) (Franklin and Dyrness 1988). Red alder and bigleaf maple (*Acer macrophyllum*) are common hardwood species.

Study sites

During the summer of 2002 we evaluated within-tree variability in isotope composition at a plantation consisting of side-by-side red alder and Douglas-fir stands near Siletz, OR (44° 44'N, 123° 52'W). Prior to planting, the site was tractor logged, scarified, and brush piles burned. Both stands contained 9-10 year old trees on a moderately well drained silt loam with a seasonal high water table and slope of 0-10%. The red alder stand had achieved crown closure, and lower branch mortality was just commencing; adjacent trees in the Douglas-fir stand were just beginning to touch.

Ten additional sites in riparian forests were selected to address within- and across- site variation in isotopic composition (Table 2.1). Five sites were dominated by Douglas-fir and 5 were dominated by red alder. All sites were located within approximately 75 km of the Pacific Ocean with a north/south range of 80 km. Study sites were selected along 2^{nd}-4^{th} order streams with relatively unconstrained reaches and monospecific overstories. Red alder dominated the canopy on red alder sites although bigleaf maple and/or conifers were sometimes minimally present. The canopy was generally closed, but not dense, and tree age ranged from roughly 30-60 years. Douglas-fir dominated the canopy in Douglas-fir sites with some occurrence of bigleaf maple, western hemlock, and western redcedar. Most sites had some red alder along the stream, but these were usually small, individual trees. No Douglas-fir site had a notable amount of upslope red alder. Tree age ranged from 40 to over 100 years old.

Table 2.1. Site characteristics.

Site	Riparian habitat	Average bankfull width (m)	Average dbh* (cm) of sampled trees	Location	Elevation (m)
Alsea tributary	Douglas-fir	1.4	59.0	44° 19' N, 123° 28' W	284
Yew Creek	Douglas-fir	3.4	46.6	44° 30'N, 123°33' W	240
Trout Creek	Douglas-fir	4.3	106.9	44° 22' N, 123° 32'W	289
South Fork of Alsea	Douglas-fir	1.2	45.8	44° 21'N, 123° 34'W	320
Wolf Creek	Douglas-fir	6.3	53.1	43° 55'N, 123° 21' W	187
Coleman Creek	red alder	7.0	27.1	44° 18' N, 123° 30' W	287
Record Creek	red alder	3.4	44.1	44° 20' N, 123° 38' W	137
Nelson Creek	red alder	6.7	43.2	44° 36'N, 123° 36' W	165
Honey Grove	red alder	4.7	37.8	44° 23' N, 123° 32' W	302
Smith Creek	red alder	5.0	31.2	43° 50' N, 123° 22'W	263

*dbh = diameter at breast height

Vegetation sampling

Plantation:

Ten red alder were sampled at 15 m intervals along two transects in the interior of the stand. At each 15 m location, the dominant tree within a 5 m radius was selected for sampling. Dominance was judged by diameter, space occupied by branches in the canopy, height, and depth of crown. One branch on the south side of each tree was clipped with pole pruners from the upper third, the middle third, and the lower third of the crown along a vertical transect. Four to five fully expanded leaves with the fewest blemishes were selected for collection from five points in the crown: (1) edge of the upper third of the canopy, (2) edge of the middle third of the canopy, (3) edge of the bottom third of the canopy, (4) mid-crown along the bottom branch, and (5) interior along the bottom branch. Leaves with small galls were not included in analysis.

The Douglas-fir stand was less accessible than the red alder stand, so the sampling protocol was modified. Ten Douglas-fir were systematically chosen for sampling in the interior of the stand. At least one tree was between each tree sampled along the plantation row. Occasionally, a tree was skipped if it did not have enough second or third year needles for a sample or if it was located near a red alder (a few of which had invaded the plantation). One branch tip on the south side of each tree was clipped with pole pruners from the upper third, middle third, and lower third of the crown making a vertical transect of the crown. First-year needles were collected from the tips of each branch cut. Second and third year needles were also collected from the middle branch. All samples were kept cold for transport to the lab.

Riparian sites:

One plot was established at each of the ten sites. Each plot extended 20 m upland from the edge of the active channel and 50 m along the stream. Five trees of the dominant canopy species were sampled per plot for foliage; 3 trees were sampled at roughly 10 m upslope from the stream at 0, 25, and 50 m from the down-stream edge of a plot, and two additional trees were sampled at roughly 0 and 20 m from the stream at 25 m from the down-stream edge of the plot. Foliage was collected with a shotgun from the middle-to-upper canopy of all trees. Approximately 50-70 first year needles from Douglas-fir and 5 fully expanded leaves from red alder were collected from each tree for a total of 5 foliage samples per site.

Sample preparation

Foliage was dried at 50° C for 48 hours and ground with mortar and pestle followed by a ball mill for 15-25 seconds into a fine powder. All equipment was wiped with acetone between each sample and samples were stored in zip-lock bags. Approximately 4 mg of red alder material and 9 mg of Douglas-fir material were weighed into tin capsules and analyzed on a continuous flow PDZ Europa

Scientific 20/20 mass spectrometer at the Berkeley Center for Stable Isotope Biogeochemistry, University of California at Berkeley for $\delta^{15}N$, %N, $\delta^{13}C$, and %C composition. Isotope values are expressed in delta notation (δ):

$$\delta X = [(R_{sample} / R_{standard}) - 1]\ 1000$$

where δX is the ratio of $^{15}N/^{14}N$ or $^{13}C/^{12}C$ compared to the international standards (atmospheric N_2 for nitrogen, Pee Dee Belemnite for C), R_{sample} is the ratio of the heavy to light isotope of the sample, and $R_{standard}$ is the ratio of the heavy to light isotope of the standard. The precision of isotope analysis was within 0.72‰ for $\delta^{15}N$ and 0.13‰ for $\delta^{13}C$ for three replicates of 9 samples.

Data analysis

Analysis of variance (ANOVA) F-tests were used to test for differences in mean isotope compositions among crown positions. A model with one main effect (position) was used to test for a position effect in $\delta^{15}N$ and $\delta^{13}C$ among crown positions at the plantation site. ANOVA F-tests were also used to test for significant differences in $\delta^{15}N$ and $\delta^{13}C$ composition among sites in riparian areas. A model with one main effect (site) was used for each comparison. Significance levels were set at ≤ 0.05 prior to the analysis. All statistical procedures were conducted using statistical software from the SAS Institute Inc. (SAS Institute Inc. 1999).

Results

Isotope variation within a tree crown: plantation site

We found different levels of variability in $\delta^{15}N$ among crown positions between Douglas-fir and red alder. In Douglas-fir, crown position had a significant effect on the $\delta^{15}N$ of needles, demonstrated by a consistent ^{15}N enrichment from the bottom to the top of the crown in first year needles by on average 2.0‰ (ANOVA F-test, $F_{1,9} = 111.4$, $p < 0.001$; Figure 2.1a). Red alder was less variable in $\delta^{15}N$

from the bottom to the top of the crown (difference of 0.28‰ on average) with no significant differences among vertical positions (ANOVA F-test, $F_{1,9} = 0.75$, $p = 0.41$; Figure 2.1b). The horizontal distribution of $\delta^{15}N$ was less variable in both species. The effect of age on $\delta^{15}N$ was significant for Douglas-fir needles along a branch (ANOVA F-test, $F_{1,9} = 41.6$, $p < 0.001$), although the difference between ages was small (0.24‰ on average). Red alder demonstrated no significant differences in $\delta^{15}N$ along a branch (ANOVA F-test, $F_{1,9} = 1.63$, $p = 0.23$).

$\delta^{13}C$ of Douglas-fir and red alder foliage increased significantly from the bottom to the top of the crown (ANOVA F-test, $F_{1,9} = 13.12$, $p < 0.01$ for Douglas-fir; $F_{1,9} = 9.77$, $p < 0.05$ for red alder; Figure 2.1). Red alder $\delta^{13}C$ was more variable across heights compared to Douglas-fir (2.12‰ average difference in red alder; 1.01‰ average difference for Douglas-fir). Neither species demonstrated significant differences in $\delta^{13}C$ along a branch into the crown interior (ANOVA F-test, $F_{1,9} = 0.07$, $p = 0.80$ for Douglas-fir needle ages; $F_{1,9} = 1.51$, $p = 0.25$ for red alder leaves along a branch).

The $\delta^{13}C$ and $\delta^{15}N$ of foliage among plantation trees demonstrated tree-to-tree variability within positions and ages. In Douglas-fir, third year needles sampled across individual trees had the least variation in $\delta^{15}N$, 1.2‰ (Figure 2.1a). First year needles from the bottom of the crown had the greatest range of $\delta^{15}N$ values across trees (range of 2.62‰) and was larger than some isotope differences across crown positions within a tree. The ranges of $\delta^{15}N$ within a position across red alder were similar for all positions and were within 0.90‰ across trees (Figure 2.1b). The variability in $\delta^{13}C$ within a position was greatest in red alder compared to Douglas-fir. Leaves from the edge of branches at the bottom of the crown were most variable and ranged in $\delta^{13}C$ by 3.4‰. First-year Douglas-fir needles sampled from the bottom of the crown also had the greatest range of isotope values within a position and varied by almost 3.3‰ across trees. There was considerable overlap among trees in the ranges of both $\delta^{13}C$ and $\delta^{15}N$ for different positions or ages.

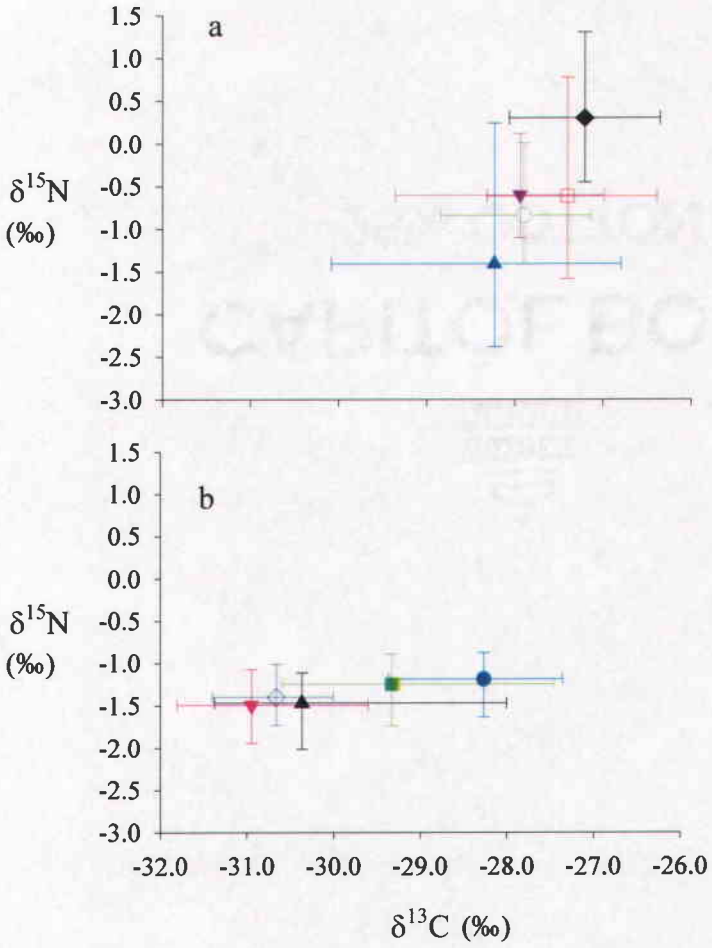

Figure 2.1. The means and ranges of the $\delta^{13}C$ and $\delta^{15}N$ composition of foliage from 10 plantation Douglas-fir (a) and red alder (b) for all five positions/ages sampled. Symbols are: a: 1 year top (◆), 1 year middle (□), 1 year bottom (▲), 2 year middle (○), 3 year middle (▼); b: edge top (●), edge middle (■), edge bottom (▲), center bottom (◇), trunk bottom (▼).

Isotope variation within a site: plantation and riparian sites

At the plantation site, foliage isotope values were averaged per tree to determine the level of isotope variation among trees on a site. Douglas-fir had greater variation in $\delta^{15}N$ among trees than red alder (Figure 2.2). Douglas-fir trees ranged by 1.72‰ in $\delta^{15}N$ while red alder trees were all within 0.74‰ across the site. Douglas-fir was also more enriched in $\delta^{15}N$ compared to red alder with an average site $\delta^{15}N$ of –0.56‰. The site average for red alder was -1.38‰. Both species had similar ranges in $\delta^{13}C$ compositions (1.70‰ and 1.52‰ for Douglas-fir and red alder, respectively); however, Douglas-fir were more enriched in ^{13}C compared to red alder.

In riparian areas, there was generally greater variation in $\delta^{15}N$ of Douglas-fir compared to red alder (Figure 2.3a). Trout Creek had the largest variation in $\delta^{15}N$ of all Douglas-fir sites with a range of 2.58‰ among trees on the site. By comparison, the maximum variation in $\delta^{15}N$ at a red alder site was 20% that of Trout Creek and occurred at Record Creek (range of 0.59‰). Only Douglas-fir at Wolf Creek and the Alsea tributary had similar ranges of $\delta^{15}N$ to that of red alder, although $\delta^{15}N$ values were not necessarily similar among the sites. $\delta^{13}C$ variation within a site was similar for red alder and Douglas-fir (Figure 2.3b). Coleman Creek had the greatest variation in $\delta^{13}C$ within a red alder site where individual trees ranged by 3.37‰. Trout Creek had the greatest variation in $\delta^{13}C$ for Douglas-fir sites and ranged by 3.29‰ across trees on the site.

Isotope variation across sites: riparian sites

Douglas-fir $\delta^{15}N$ varied significantly among riparian sites (ANOVA F-test, $F_{4, 20} = 7.27$, $p < 0.001$). Individual trees ranged in $\delta^{15}N$ by up to 3.5‰ (Figure 2.3), although the average site $\delta^{15}N$ varied by half as much (Figure 2.4). Conversely, differences among red alder sites were not significant (ANOVA F-test, $F_{4, 20} = 1.96$, $p = 0.14$). Red alder trees ranged between –1.5‰ and –0.5‰, and

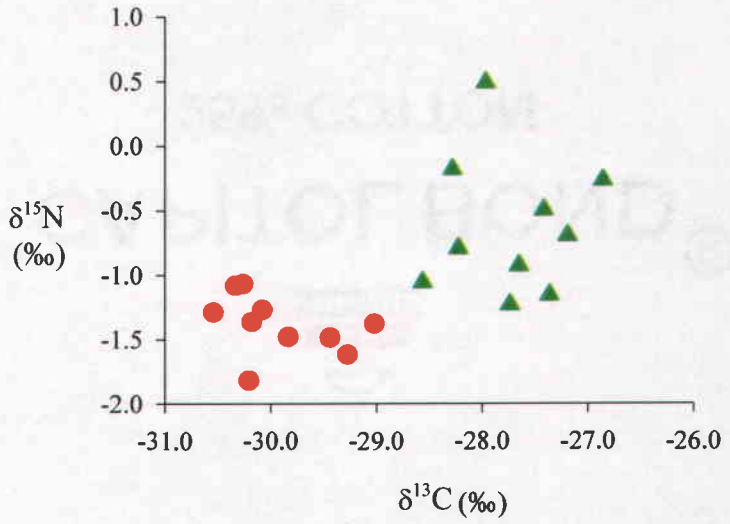

Figure 2.2. The average $\delta^{13}C$ and $\delta^{15}N$ of foliage samples from 10 red alder (●) and 10 Douglas-fir (▲) trees from adjacent plantation stands.

average site differences in $\delta^{15}N$ were within 0.27‰. The $\delta^{15}N$ of Douglas-fir across sites encompassed the range of red alder $\delta^{15}N$, although most trees were either similar to, or heavier than, red alder. Trout and South Fork Creeks had site $\delta^{15}N$ averages almost indistinguishable from those of red alder while all the trees sampled in Wolf and Yew Creeks were more depleted in ^{15}N. Overall, trees on Douglas-fir sites were more depleted in ^{15}N compared to red alder (Figure 2.4).

Red alder and Douglas-fir had similar levels of variation in $\delta^{13}C$ across sites although only Douglas-fir sites had significant differences (ANOVA F-test, $F_{4, 20} = 3.18$, $p = 0.04$ for Douglas-fir; $F_{4, 20} = 2.72$, $p = 0.06$ for red alder; Figure 2.4). Red alder was generally more depleted in ^{13}C than Douglas-fir with one tree reaching almost –31.0‰. Douglas-fir $\delta^{13}C$ remained above -29.0‰. Red alder leaves were all below –26.5‰ while Douglas-fir had several trees across sites above this value.

Isotope distinction between Douglas-fir and red alder

At the plantation site, Douglas-fir and red alder trees separated into two groups when $\delta^{13}C$ and $\delta^{15}N$ were both used, although the amount of separation was small (Figure 2.2). The average $\delta^{15}N$ of both species overlapped, and the average $\delta^{13}C$ of some trees were separated by less than 1.0‰. Douglas-fir tended to be more enriched in both ^{13}C and ^{15}N compared to red alder.

In riparian areas, the average $\delta^{13}C$ and $\delta^{15}N$ for each site demonstrated some level of separation between Douglas-fir and red alder sites, but the amount of separation was site specific (Figure 2.4). Trout and South Fork Creeks were most similar to red alder sites in isotope composition for both nitrogen and carbon. The remaining three Douglas-fir sites were all depleted in ^{15}N compared to red alder sites.

Discussion

Variation in $\delta^{15}N$

The most striking difference between red alder and Douglas-fir at the plantation site was the level of variation in the $\delta^{15}N$ among trees. The range of variation in Douglas-fir $\delta^{15}N$ was over four times greater within a tree crown than observed for red alder. Douglas-fir was progressively enriched in ^{15}N from the bottom to the top of the crown with 85% greater vertical difference in $\delta^{15}N$ compared to red alder. Horizontal position in the crown was less important than vertical position for both species, although Douglas-fir exhibited small significant differences between needle ages. Other studies of crown variation in $\delta^{15}N$ found either no significant differences in $\delta^{15}N$ among foliage from different crown positions or a slight enrichment in ^{15}N from the bottom to the top of the crown (Domenach et al. 1989, Gebauer and Schulze 1991, Garten 1993).

There was also considerable tree-to-tree variation in $\delta^{15}N$ for a particular crown position that was frequently greater than the average isotope differences

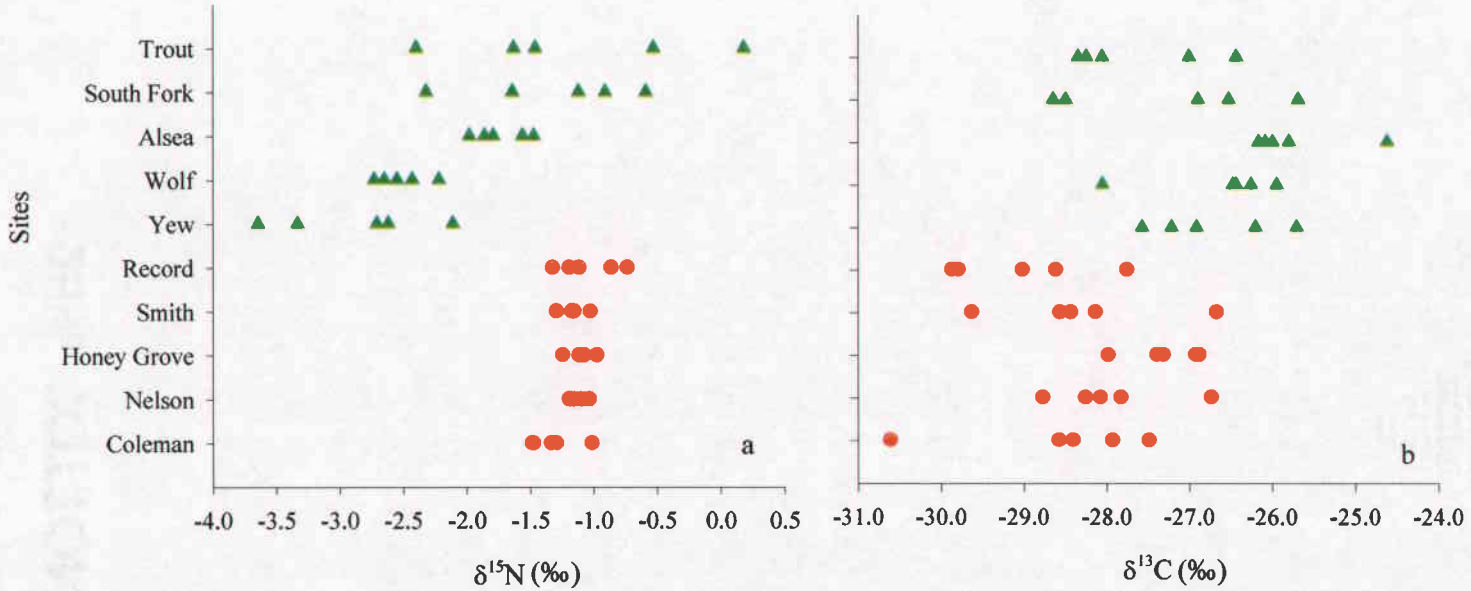

Figure 2.3. The $\delta^{15}N$ (a) and $\delta^{13}C$ (b) of Douglas-fir (▲) and red alder (●) trees across riparian sites. Each point represents an individual tree.

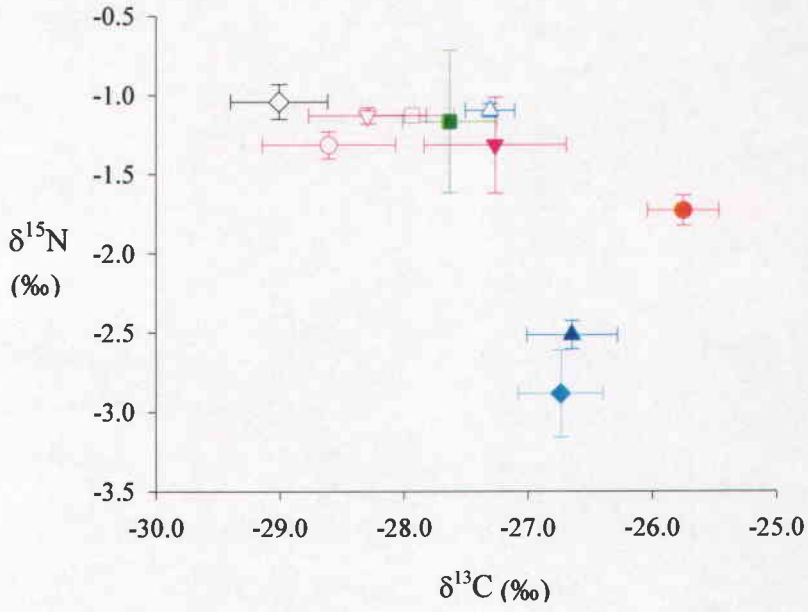

Figure 2.4. The average $\delta^{15}N$ and $\delta^{13}C$ foliage of five trees sampled per site (+/- 1 standard error). Douglas-fir sites are filled shapes; red alder sites are open shapes. Sites are: Alsea (●), Trout (■), Wolf (▲), South Fork (▼), Yew (◆), Coleman (○), Nelson (□), Honey Grove (△), Smith (▽), Record (◇).

across vertical position or needle age. Within a tree, though, the $\delta^{15}N$ across positions tended to track together such that a tree with relatively more enriched foliage at the top of the crown also tended to have relatively more enriched foliage in other crown positions. This was especially true of the $\delta^{15}N$ for Douglas-fir needles.

In riparian areas, Douglas-fir and red alder demonstrated similar patterns in $\delta^{15}N$ as found at the plantation. Douglas-fir sites generally had greater within-site variation in $\delta^{15}N$ among trees compared to red alder sites (Figure 2.3a). Across all riparian locations, only Douglas-fir sites had significant differences in average $\delta^{15}N$. The average $\delta^{15}N$ of Yew and Wolf Creeks were noticeably more depleted in ^{15}N than the remaining three sites, which were closer to the average $\delta^{15}N$ of red alder sites (Figure 2.4). Red alder sites were all similar in $\delta^{15}N$ and had < 0.5‰ variation in $\delta^{15}N$ around -0.14‰.

In this study, there were two common themes in $\delta^{15}N$ between red alder and Douglas-fir across all the comparisons made: 1) red alder consistently had less variation in $\delta^{15}N$ than Douglas-fir, and 2) the $\delta^{15}N$ of red alder was always near -1.0‰ to -1.5‰ while Douglas-fir $\delta^{15}N$ varied depending on location on a site or across sites. The combined consistency in both $\delta^{15}N$ variation and composition for red alder suggests it was acquiring most of its nitrogen from a common source, N-fixation. Plants that fix N generally have $\delta^{15}N$ between –2.0‰ and 2.0‰ that reflect atmospheric $\delta^{15}N$, which equals zero (Shearer and Kohl 1986). Red alder is known to fix N at high rates ranging up to 200 kg $ha^{-1}yr^{-1}$ in the Oregon Coast Range (Binkley et al. 1994). In greenhouse studies, the $\delta^{15}N$ of alder species grown in N-free media were between 0‰ and –2.0‰ (Binkley et al. 1985, Domenach et al. 1989, Hurd et al. 2001) and served as an isotope comparison to determine the level of N-fixation by alder in the field (Beaupied et al. 1990, Hurd et al. 2001). Using $\delta^{15}N$, Beaupied et al. (1990) and Hurd et al. (2001) found similar

foliage $\delta^{15}N$ in alder and predicted upwards of 85% of their N was derived from fixation.

By comparison, the high variability of Douglas-fir $\delta^{15}N$ within and among sites may be explained by the dependence of Douglas-fir on soil N. The $\delta^{15}N$ of soil N pools can have high spatial variability both horizontally (Bundt et al. 2001) and vertically (Nadelhoffer and Fry 1988, Bundt et al. 2001) across small scales and can vary depending on the rate of nutrient cycling at a particular site (Garten and Van Miegroet 1994). Additionally, mycorrhizal associations (Hobbie and Colpaert 2003), site history (Koerner et al. 1999), topography (Garten 1993, Sutherland et al. 1993), and different forms of soil N can further influence foliage $\delta^{15}N$ at a site (Evans 2001). Fire has been shown to enrich the $\delta^{15}N$ of post-fire vegetation compared to unburned sites due to the consumption of ^{15}N depleted litter layers at the soil surface and increased nitrification rates (Högberg 1997, Grogan et al. 2000). In riparian areas, microbial denitrification in anoxic areas can make soil $\delta^{15}N$ of inorganic N especially variable (Hedin et al. 1998). Any number of these factors may have influenced the variability in $\delta^{15}N$ composition among Douglas-fir trees at plantation and riparian sites. For example, the heavier average $\delta^{15}N$ of plantation Douglas-fir compared to riparian trees may have resulted from site preparation methods involving brush pile burning. The lack of differences between the $\delta^{15}N$ of plantation red alder and those in riparian areas again suggests nitrogen fixation was the primary means of N acquisition for this species in both habitats. Despite the high potential for variation in soil $\delta^{15}N$, two Douglas-fir sites, Wolf Creek and the Alsea tributary, demonstrated levels of $\delta^{15}N$ variation similar to those of red alder sites and may indicate the presence of fairly homogenous N pools (Grogan et al. 2000). In addition to soil influences on tree $\delta^{15}N$ heterogeneity, genetic differences among trees may also contribute to tree-to-tree variability (reviewed by Robinson 2001, Dawson et al. 2002).

Although it is likely red alder was acquiring the majority of its nitrogen through fixation, this cannot be determined conclusively because of the similarity

of the $\delta^{15}N$ composition of Douglas-fir needles from some trees and some sites with red alder leaves. In both plantation and riparian areas, the range of average $\delta^{15}N$ values for Douglas-fir overlapped that of red alder. The similarity of the two species in $\delta^{15}N$ composition suggests the soil $\delta^{15}N$ composition of plant-available nitrogen was sufficiently similar to that of the atmosphere to make distinguishing between the two sources difficult (Shearer and Kohl 1986, Högberg 1997). The history of past red alder distribution across the sites may be a driving factor influencing the soil $\delta^{15}N$ composition, especially because of the strong influence red alder can have on soil properties. Increased soil N content as well as rates of nutrient cycling and nitrification (Binkley et al. 1992, Bormann et al. 1994) all result from the presence of red alder and may persist once the species is no longer present (Wigington et al. 1998). Red alder is common in riparian areas in the Oregon Coast Range (Nierenberg and Hibbs 2000), and although red alder was virtually absent on Douglas-fir sites at the time of sampling, prior site occupancy of red alder may have contributed to soil N heterogeneity both within and across sites. This may explain the close agreement of the average $\delta^{15}N$ composition of two Douglas-fir sites (Trout Creek and South Fork) with red alder sites. The influence of historic red alder may not have been as intense at the remaining Douglas-fir sites. For our purposes, it is not necessary to determine whether or not red alder was fixing the majority of its nitrogen. Rather, the consistency of the $\delta^{15}N$ composition of red alder makes it relatively easy to identify a "characteristic" $\delta^{15}N$ signature that may be useful in food web analysis. In contrast, the greater variability in $\delta^{15}N$ composition of Douglas-fir made it more difficult to identify a single or narrow range of $\delta^{15}N$ values indicative of the species across a range of sites.

Nitrogen source heterogeneity can account for much of the variability in $\delta^{15}N$ among Douglas-fir, but it does not necessarily address the variation in $\delta^{15}N$ within the crown of a tree. It is unclear what caused $\delta^{15}N$ gradients found in Douglas-fir, but it may be related to light gradients in the crown and their affect on

foliar N concentration and N allocation. Foliage in high light environments has demonstrated higher N content (Brooks et al. 1996), lower chlorophyll to nitrogen ratios (Brooks et al. 1996, Warren and Adams 2001, Warren et al. 2003), and higher Rubisco to chlorophyll ratios (Warren and Adams 2001, Warren et al. 2003) compared to foliage in more shaded environments. Proteins, such as Rubisco, are more enriched in ^{15}N compared to other plant compounds like chlorophyll (Werner and Schmidt 2002). The foliar $\delta^{15}N$ gradient we found in Douglas-fir may reflect a greater allocation of N to proteins relative to other plant compounds in needles of different canopy heights, hence light environments, although this is only speculation. Further research is needed to better understand the mechanism(s) structuring $\delta^{15}N$ in Douglas-fir needles.

Variation in $\delta^{13}C$

Red alder and Douglas-fir were significantly enriched in ^{13}C from the bottom to the top of the crown, although the pattern was more pronounced in red alder. This trend was similar to findings in other canopy studies (Figure 2.1; Garten and Taylor 1992, Buchmann et al. 1997, Le Roux et al. 2001, Fessenden and Ehleringer 2002, Fessenden and Ehlerginger 2003). Red alder leaves from the top and the bottom of the crown differed by almost 2.5‰ on average whereas Douglas-fir needles differed by roughly 1.0‰ on average between the same positions. Horizontal position did not significantly influence the $\delta^{13}C$ for either species although interior leaves tended to be more depleted than exterior leaves. Within a crown position, there was tree-to-tree variability in $\delta^{13}C$ that could be over 3.0‰ for both species. In general, the $\delta^{13}C$ of plantation Douglas-fir was more enriched in ^{13}C compared to red alder such that the two species were isotopically distinct when all crown positions were averaged per tree (Figure 2.2).

In riparian areas, Douglas-fir and red alder sites had similar levels of variation in $\delta^{13}C$ among trees on a site (Figure 2.3b). All sites demonstrated at least a 1.0‰ difference in $\delta^{13}C$ composition among trees of both species, although

the greatest range of $\delta^{13}C$ among trees was at a red alder site. Across riparian sites, only Douglas-fir demonstrated significant differences in mean $\delta^{13}C$; however, the variance among red alder sites was only slightly less than that of Douglas-fir sites. Douglas-fir were generally more enriched in ^{13}C than red alder across sites although the difference in $\delta^{13}C$ values between the two species was small (Figure 2.4).

The $\delta^{13}C$ of Douglas-fir and red alder at plantation and riparian sites offered two broad levels of interpretation for how each species was responding to the environment. First, $\delta^{13}C$ suggested species differences in water-use efficiency (ratio of carbon acquired to water vapor lost through stomatal conductance; Farquhar et al. 1982, Dawson et al. 2002) by the consistent enrichment of Douglas-fir in ^{13}C compared to red alder. Species with more efficient water-use discriminate less against ^{13}C during photosynthesis by increasing stomatal regulation in response to increased transpiration. The resulting reduction in gas exchange with the atmosphere leads to a greater dependence on CO_2 in intercellular air spaces such that $^{13}CO_2$ is more frequently assimilated despite a preference for the lighter isotope by the photosynthetic machinery (see Farquhar et al. 1982 for more detailed explanation). Evergreen species are typically more enriched in ^{13}C compared to deciduous species, which has been attributed to greater water-use efficiency (Garten and Taylor 1992, Marshall and Zhang 1994), and Douglas-fir has demonstrated greater tolerance for water-limiting conditions compared to red alder (Chan et al. 2003). Additionally, morphological differences influencing hydraulic conductivity through xylem (Ponton et al. 2000), leaf shape, and stomatal density all influence water-use efficiency, hence $\delta^{13}C$, and may have contributed to the $\delta^{13}C$ differences found between Douglas-fir and red alder (reviewed by Dawson et al. 2002). The different water-use efficiencies of the two species may allow for species distinction that could be useful for food web analysis, although only at the plantation site were Douglas-fir and red alder distinct in $\delta^{13}C$ composition and even then by less than 0.5‰.

Second, the variation in $\delta^{13}C$ within each species reflected the individual environmental, and possibly genetic, conditions of each tree within and across sites. Although it is beyond the scope of this study to elucidate exact mechanisms for the observed variability in $\delta^{13}C$ found (see review by Dawson et al. 2002), it is likely light gradients within tree crowns influenced the enrichment of foliage in ^{13}C from the bottom to the top of the crown in plantation trees. Decreasing light availability with crown depth can reduce rates of photosynthesis leading to greater discrimination against ^{13}C in carbon assimilation (hence a more depleted $\delta^{13}C$ low in the crown; Garten and Taylor 1992, Le Roux et al. 2001). All of our foliage samples were taken from the same aspect to minimize variations from differential sun exposure (Waring and Silvester 1994), but invariably foliage at the top of the canopy was exposed to more light compared to foliage further down in the crown. Although gradients in the $\delta^{13}C$ of CO_2 within forest canopies can also influence the $\delta^{13}C$ of foliage across different height positions (Sternberg et al. 1989, Buchmann et al. 1997, Le Roux et al. 2001), light is generally thought to be more influential (Le Roux et al. 2001).

Additional environmental factors other than light likely played a stronger role in influencing $\delta^{13}C$ variation among trees in the plantation and riparian areas, especially moisture availability. Moisture availability can influence the $\delta^{13}C$ of trees by increasing discrimination against ^{13}C when moisture is readily available causing $\delta^{13}C$ to become more negative (Farquhar et al. 1982, Stewart et al. 1995). The $\delta^{13}C$ of plantation trees was generally more enriched than that of riparian trees, which suggests the plantation had greater water availability. Plantation soil was moderately well drained and had a seasonal high water table, which likely contributed to greater soil moisture. It is possible competition for water resources in the riparian environment with understory species required trees to use water more efficiently and contributed to the more positive $\delta^{13}C$ values. Differences in tree size may also have contributed to the more enriched $\delta^{13}C$ composition of riparian trees that resulted from increased hydraulic resistance through taller stems

and longer branches in the mature riparian trees (Panek and Waring 1995). Within riparian sites, moisture variability depending on tree location on the plot may have influenced the water availability for each tree and contributed to the $\delta^{13}C$ variation found, although our results showed no strong relationships with the approximate distance from, or height above, the stream (data not shown; Stewart et al. 1995). Across riparian sites, Douglas-fir and red alder demonstrated similar ranges in $\delta^{13}C$ variation which may reflect more general moisture conditions common to riparian areas of the Oregon Coast Range. The $\delta^{13}C$ of plant communities experiencing similar precipitation levels have been shown to be good indicators of the water availability of a system (Stewart et al. 1995). Other studies conducted in western Oregon and Washington for Douglas-fir found similar $\delta^{13}C$ values for Douglas-fir needles (Panek and Waring 1995, 1997, Fessenden and Ehleringer 2002) as this study and may indicate a characteristic range of Douglas-fir $\delta^{13}C$ values for this area. No such similar comparison exists for red alder.

Isotope variation across all three scales

This study explored three scales of potential isotope variation in Douglas-fir and red alder to determine the level of consistency in isotope composition within each species. Our results demonstrated that the level of consistency in isotope composition depended on the species of interest, the isotope being investigated, and the scale of analysis. For example, Douglas-fir had significant differences in mean $\delta^{15}N$ composition among vertical crown positions that, if not controlled for, could increase the variation in $\delta^{15}N$ found within and across sites. Collecting foliage from similar crown heights would be critical for minimizing $\delta^{15}N$ variation in Douglas-fir samples at larger scales, although collecting similar aged needles may be less important for reducing $\delta^{15}N$ variation. Conversely, the consistency of red alder $\delta^{15}N$ composition within a tree crown suggests sampling trees from similar heights is less crucial for this species to reduce $\delta^{15}N$ variation within and across sites. The variation in mean $\delta^{13}C$ composition within a tree crown had similar

implications for influencing isotope variability within a site to that of nitrogen except that red alder was as susceptible to isotope variations as Douglas-fir. It is possible the disparity of $\delta^{13}C$ across crown positions of both species is higher in larger trees, such as those at our riparian sites, where there is a greater distance between crown positions. However, Fessenden and Ehleringer (2002) found only 1.0‰ to 2.0‰ difference between the $\delta^{13}C$ composition of Douglas-fir needles from the top and middle portions of the canopy in 20 and 450 year old trees. No information was available for red alder. Again, sampling from similar heights would help minimize mean $\delta^{13}C$ variation within and across sites as long as the light environment at the sampling position was also alike (Garten and Taylor 1992). Waring and Silvester (1994) and Panek and Waring (1995) also caution to sample along similar branch positions. Additionally, similar moisture environments would be important for minimizing $\delta^{13}C$ variation within and across sites.

Adequacy of species differences for food web analysis

For natural abundance stable isotopes to be useful in tracing the fates and transformations of resources in an ecosystem, the isotope signatures of those sources must be distinguishable from each other (Peterson and Fry 1987, Robinson 2001, Dawson et al. 2002). Previous studies using natural abundance stable isotopes have utilized sources with isotopic differences of roughly 10‰ or greater that result from different photosynthetic pathways of vegetation (C3 versus C4 or CAM; Peterson and Fry 1987, Hobson 1995, Cerling et al. 1999), marine inputs to terrestrial systems (Bilby et al. 1996, Helfield and Naiman 2001), and terrestrial versus aquatic origins for material (Rounick and Winterbourn 1986), although smaller isotope differences between sources have also been used (Sydeman et al. 1997). Stable isotopes have also been used to determine the amount of nitrogen derived from the atmosphere in N_2-fixing plants, although Högberg (1997) cautioned these estimates were most reliable when there was at least a 5‰ difference between the $\delta^{15}N$ of reference and N_2-fixing plants.

In food web analysis, the isotope composition of food sources and consumer tissues are compared to determine the relative importance of different sources to a consumer's diet (Phillips and Gregg 2001). The greater the similarity in isotopic signatures of a food source with the consumer, after accounting for trophic fractionation and elemental concentration in the sources (Phillips and Koch 2002), suggests a greater contribution of that source to the consumer's diet. Typically, successive trophic levels are enriched in ^{15}N by 3.4‰ (DeNiro and Epstein 1981, Ponsard and Arditi 2000, Post 2002) although the enrichment can range from 2.0‰ to 5.0‰ (Peterson and Fry 1987, Post 2002). Carbon signatures are generally conserved between consumers and sources with a trophic fractionation of <1.0‰ (DeNiro and Epstein 1978, Peterson and Fry 1987, Post 2002). This additional trophic fractionation may further obfuscate consumer-source relationships, especially when source isotope signatures are already similar in nature.

Phillips and Gregg (2001) explored several levels of isotopic differentiation in sources to determine the minimum isotopic difference required to estimate the proportions of specific sources in a mixture (i.e., a consumer). They determined that the amount of variance in the source signatures, the variance in the consumer signature, and the sample size were most influential in distinguishing two sources. As source isotopic variation decreased and the sample size increased, the ability to accurately predict the proportion of a consumer's diet from specific sources increased. Increasing the sample size of consumers would also better determine which food source was of greater import. Additionally, increasing the isotopic difference between sources from 2.0‰ to 4.0‰ reduced the uncertainty of the source proportion estimate by half.

High isotope variability can limit the usefulness of averages to adequately represent the isotope composition of sources and make comparisons with other sources more difficult. For example, the Douglas-fir site at Trout Creek had an average $\delta^{15}N$ that placed it similar to the $\delta^{15}N$ of red alder sites, but two of the trees

were outside the range of red alder $\delta^{15}N$ for individual trees by +/- 0.90‰. Using the average in this case loses important information that not all trees are similar to red alder $\delta^{15}N$. This suggests that the average $\delta^{15}N$ for Trout Creek may not be representative of the $\delta^{15}N$ of that site. For red alder, though, the consistency in $\delta^{15}N$ within a site suggested the trees sampled adequately represented the $\delta^{15}N$ signature of each site. Reduced variation in source isotope composition can also better identify subtle differences between sources that may be important in food web analysis. In riparian areas, the $\delta^{13}C$ of Douglas-fir and red alder varied by more than 1.0‰ within a site and overlapped in isotope values, although species differences in $\delta^{13}C$ were still apparent. If the level of variation in $\delta^{13}C$ within each species had been lower, it is possible there would have been greater species separation, which would be easier to follow through a food web.

The difference between the $\delta^{15}N$ and $\delta^{13}C$ signatures of red alder and Douglas-fir at our study sites were, on average, less than 2.0‰, so it is unlikely stable isotopes could be broadly used as an effective tool for determining the contributions of Douglas-fir versus red alder to food webs in this system. However, our two Douglas-fir sites on Yew and Wolf Creeks were clearly distinct from red alder sites, especially in $\delta^{15}N$ composition, even though the difference between them was on average just over 1.0‰ (Figure 2.4). This suggests it may be possible to conduct site-specific research in the Oregon Coast Range using stable isotopes in a food web analysis at specific sites where the mean isotopic composition of Douglas-fir and red alder are distinct.

Conclusions

Douglas-fir and red alder demonstrated species specific trends in isotope composition that have potential use for food web analysis. However, the limited separation in $\delta^{13}C$ and $\delta^{15}N$ composition between the species suggests linking consumers to red alder versus Douglas-fir as the base of a food web may be tenuous unless careful measures are taken to reduce isotope variability within the

sources. Sampling foliage from consistent tree heights and light regimes, as well as identifying specific sites where differences in isotope signatures are maximized between the species may help increase species distinctions. Even though stable isotopes of nitrogen and carbon may not be appropriate for broad use in riparian areas of the Oregon Coast Range, they may still provide useful information for food webs in Douglas-fir-and red alder-dominated riparian areas. In addition to acting as a potential tracer through a food web, the trophic position of an organism can be determined by the amount of fractionation in the $\delta^{15}N$ composition between it and the base of the food web (Vander Zanden and Rasmussen 1999, Post 2002). Greater trophic fractionation implies more steps along the food web and possibly a more diverse ecosystem. The trophic position of an organism sampled at a red alder- versus Douglas-fir-dominated riparian area may provide some insight into the complexity of the food web in each system. This could have important bearings on the trade-offs of converting hardwood dominated riparian areas to those dominated by conifers.

References

Allan, J.D., M.S. Wipfli, J.P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences 60: 309-320.

Beaupied, H., A. Moiroud, A. Domenach, F. Kurdali, and R. Lensi. 1990. Ratio of fixed and assimilated nitrogen in a black alder (*Alnus glutinosa*) stand. Canadian Journal of Forest Research 20: 1116-1119.

Ben-David, M., R.W. Flynn, and D.M. Schell. 1997. Annual and seasonal changes in diets of martens; evidence from stable isotope analysis. Oecologia 111: 280-291.

Bilby, R.E., B.R. Fransen, and P.A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53: 164-173.

Binkley, D., K. Cromack, Jr., and D.D. Baker. 1994. Nitrogen fixation by red alder: biology, rates, and controls. Pages 57-72 *in* D.E. Hibbs, D.S. DeBell, and R.F. Tarrant, editors. The biology and management of red alder. Oregon State University Press, Corvallis, OR.

Binkley, D., P. Sollins, R. Bell, D. Sachs, and D. Myrold. 1992. Biogeochemistry of adjacent conifer and alder-conifer stands. Ecology 73: 2022-2033.

Binkley, D., P. Sollins, and W.B. McGill. 1985. Natural abundance of nitrogen-15 as a tool for tracking alder-fixed nitrogen. Soil Science Society of America Journal 49: 444-447.

Bormann, B.T., K. Cromack, Jr., and W.O. Russell III.1994. Influences of red alder on soils and long-term ecosystem productivity. Pages 47-56 *in* D.E. Hibbs, D.S. DeBell, and R.F. Tarrant, editors. The biology and management of red alder. Oregon State University Press, Corvallis, OR.

Brooks, J.R., D.G. Sprugel, and T.M. Hinckley. 1996. The effects of light acclimation during and after foliage expansion on photosynthesis and *Abies amabilis* foliage within the canopy. Oecologia 107: 21-32.

Buchmann, N., W. Kao, and J. Ehleringer. 1997. Influence of stand structure on carbon-13 of vegetation, soils, and canopy air within deciduous and evergreen forests in Utah, United States. Oecologia 110: 109-119.

Bundt, M., M. Jaggi, P. Blaser, R. Siegwolf, and F. Hagedorn. 2001. Carbon and nitrogen dynamics in preferential flow paths and matrix of a forest soil. Soil Science Society of America Journal 65: 1529-1538.

Cerling, T.E., J.M Harris, M.G. Leakey. 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. Oecologia 120: 364-374.

Chan, S.S., S.R. Radosevich, and A.T. Grotta. 2003. Effects of contrasting light and soil moisture availability on the growth and biomass allocation of Douglas-fir and red alder. Canadian Journal of Forest Research 33: 106-117.

Cherel, Y., K.A. Hobson, and H. Weimerskirch. 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122: 155-162.

Dawson, T.E., S. Mambelli, A.H. Planboeck, P.H. Templer, and K.P. Tu. 2002. Stable isotopes in plant ecology. Annual Review of Ecology and Systematics 33: 507-559.

DeNiro, M.J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42: 495-506.

DeNiro, M.J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45: 341-351.

Domenach, A.M., F.Kurdali, and R. Bardin. 1989. Estimation of symbiotic dinitrogen fixation in alder forest by the method based on natural ^{15}N abundance. Plant and Soil 118: 51-59.

Evans, R.D. 2001. Physiological mechanisms influencing plant nitrogen isotope composition. Trends in Plant Science 6: 121-126.

Farquhar, G.D., M.H. O'Leary, and J.A. Berry. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology 9: 121-137.

Fessenden, J.E., and J.E. Ehleringer. 2002. Age-related variations in $\delta^{13}C$ of ecosystem respiration across a coniferous forest chronosequence in the Pacific Northwest. Tree Physiology 22: 159-167.

Fessenden, J.E., and J.E. Ehleringer. 2003. Temporal variation in $\delta^{13}C$ of ecosystem respiration in the Pacific Northwest: links to moisture stress. Oecologia 136: 129-136.

Franklin, J.F., and C.T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press. Corvallis.

Garten, Jr., C.T. 1993. Variation in foliage ^{15}N abundance and the availability of soil nitrogen on Walker Branch Watershed. Ecology 74: 2098-2113.

Garten, Jr., C.T., and G.E. Taylor, Jr. 1992. Foliage $\delta^{13}C$ within a temperate deciduous forest: spatial, temporal, and species sources of variation. Oecologia 90: 1-7.

Garten, Jr., C.T., and H. Van Miegroet. 1994. Relationships between soil nitrogen dynamics and natural ^{15}N abundance in plant foliage from Great Smoky Mountains National Park. Canadian Journal of Forest Research. 24: 1636-1645.

Gebauer, G., and E.D. Schulze. 1991. Carbon and nitrogen isotope ratios in different compartments of a healthy and a declining *Picea abies* forest in the Fichtelgebirge, NE Bavaria. Oecologia 87: 198-207.

Gregory, S.V., F.J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. Focus on links between land and water. Bioscience 8: 540-551.

Grogan, P., T.D. Bruns, and F.S. Chapin III. 2000. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. Oecologia 122: 537-544.

Hedin, L.O., J.C. von Fischer, N.E. Ostrom, B.P. Kennedy, M.G. Brown, and G.P. Robertson. 1998. Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil-stream interfaces. Ecology 79: 684-703.

Helfield, J.M., and R.J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology 82: 2403-2409.

Herrera M., L.G., K.A. Hobson, L. Miron M., N. Ramirez P., G. Mendez C., and V. Sanchez-Cordero. 2001. Sources of protein in two species of phytophagous bats in a seasonal dry forest: evidence from stable-isotope analysis. Journal of Mammalogy 82: 352-361.

Hobbie, E.A., and J. V. Colpaert. 2003. Nitrogen availability and colonization by mycorrhizal fungi correlate with nitrogen isotope patterns in plants. New Phytologist 157: 115-126.

Hobson, K.A. 1995. Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. The Condor 97: 752-762.

Högberg, P. 1997. Tansley Review No. 95. ^{15}N natural abundance in soil-plant systems. New Phytologist 137: 179-203.

Hurd, T.M., D.J. Raynal, C.R. Schwintzer. 2001. Symbiotic N_2-fixation of *Alnus incana* ssp. *rugosa* in shrub wetlands of the Adirondack Mountains, New York, USA. Oecologia 126: 94-103.

Koerner, W., E. Dambrine, J.L. Dupouey, and M. Benoît. 1999. $\delta^{15}N$ of forest soil and understorey vegetation reflect the former agricultural land use. Oecologia 121: 421-425.

Le Roux, X., T. Bariac, H. Sinoquet, B. Genty, C. Piel, A. Mariotti, C. Girardin, and P. Richard. 2001. Spatial distribution of leaf water-use efficiency and carbon isotope discrimination within an isolated tree crown. Plant, Cell, and Environment 24: 1021-1032.

Marshall, J.D., and J. Zhang. 1994. Carbon isotope discrimination and water-use efficiency in native plants of the north-central Rockies. Ecology 75: 1887-1895.

McComb, W.C. 1994. Red alder: interactions with wildlife. *In* The biology and management of red alder. Pages 131-138 *in* D.E. Hibbs, D.S. DeBell, and R.F. Tarrant, editors. The biology and management of red alder. Oregon State University Press, Corvallis, OR.

McIlwee, A.P., and C.N. Johnson. 1998. The contribution of fungus to the diets of three mycophagous marsupials in *Eucalyptus* forests, revealed by stable isotope analysis. Functional Ecology 12: 223-231.

Nadelhoffer, K.J., and Fry, B. 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Science Society of America Journal 52: 1633-1640.

Nierenberg, T.R., and D.E. Hibbs, 1999. A characterization of unmanaged riparian areas in the central Coast Range of western Oregon. Forest Ecology and Management 129: 195-206.

Orr, E.L., W.N. Orr, and E.M. Baldwin. 1992. Geology of Oregon. Fourth edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Panek, Jeanne A. and R.H. Waring. 1995. Carbon isotope variation in Douglas-fir foliage: improving the $\delta^{13}C$-climate relationship. Tree Physiology 15: 657-663.

Panek, Jeanne A. and R.H. Waring. 1997. Stable carbon isotopes as indicators of limitations to forest growth imposed by climate stress. Ecological Applications. 7: 854-863.

Peterson, B.J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecological Systems 18: 293-320.

Phillips, D.L. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. Oecologia 127: 166-170.

Phillips, D.L., and J.W. Gregg. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127: 171-179.

Phillips, D.L., and P.L. Koch. 2002. Incorporating concentration dependence in stable isotope mixing models. Oecologia 130: 114-125.

Polischuk, S.C., K.A. Hobson, and M.A. Ramsay. 2001. Use of stable-carbon and – nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. Canadian Journal of Zoology 79: 499-511.

Ponsard, S., and R. Arditi. 2000. What can stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) tell about the food web of soil macro-invertebrates? Ecology 81: 852-864.

Ponton, S., J.-L. Dupouey, N. Breda, F. Feuillat, C. Bodenes, and E. Dreyer. 2001. Carbon isotope discrimination and wood anatomy variations in mixed stands of *Quercus robur* and *Quercus petraea*. Plant, Cell and Environment 24: 861-868.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703-718.

Robinson, D. 2001. $\delta^{15}N$ as an integrator of the nitrogen cycle. Trends in Ecology and Evolution 16: 153- 162.

Rounick, J.S. and M.J. Winterbourn. 1986. Stable carbon isotopes and carbon flow in ecosystems. BioScience 36: 171-177.

SAS Institute Inc. (1999). SAS OnlineDoc, Version 8 Edition. Cary, NC.

Shearer, G., and D.H. Kohl. 1986. N_2-fixation in field settings: estimations based on natural ^{15}N abundance. Australian Journal of Plant. Physiology 13: 699-756.

Sternberg, L., S.S. Mulkey, and S.J. Wright. 1989. Ecological interpretation of leaf carbon isotope ratios: influence of respired carbon dioxide. Ecology 70: 1317-1324.

Stewart, G.R., M.H. Turnbull, S. Schmidt, and P.D. Erskine. 1995. ^{13}C natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. Australian Journal of Plant Physiology 22: 51-55.

Sutherland, R.A., C. van Kessel, R.E. Farrell, and D.J. Pennock. 1993. Landscape-scale variations in plant and soil nitrogen-15 natural abundance. Soil Science Society of America Journal 57: 169-178.

Sydeman, W.J., K.A. Hobson, P. Pyle, and E.B. McLaren. 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. The Condor 99: 327-336.

Tieszen, L.L., T.W. Boutton, K.G. Tesdahl, and N.A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia 57: 32-37.

Vander Zanden, M.J., and J.B. Rasmussen. 1999. Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology 80: 1395-1404.

Warren, C.R., and M.A. Adams. 2001. Distribution of N, Rubisco and photosynthesis in *Pinus pinaster* and acclimation to light. Plant, Cell and Environment 24: 597-609.

Warren, C.R., G.J. Ethier, N.J. Livingston, N.J. Grant, D.H. Turpin, D.L. Harrison, and T.A. Black. 2003. Transfer conductance in second growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.)Franco) canopies. Plant, Cell and Environment 26: 1215-1227.

Waring, R.H. and W.B. Silvester. 1994. Variation in foliage $\delta^{13}C$ values within the crowns of *Pinus radiata* trees. Tree Physiology 14: 1203-1213.

Wigington, Jr., P.J., M.R. Church, T.C. Strickland, K.N. Eshleman, and J. Van Sickle. 1998. Autumn chemistry of Oregon Coast Range streams. Journal of American Water Resources Association 34: 1035-1049.

Wipfli, M.S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 54: 1259-1269.

Wolf, B., Martinez del Rio, C. 2000. Use of saguaro fruit by white-winged doves: isotopic evidence of a tight ecological association. Oecologia 124: 536-543.

SOURCE-SINK RELATIONSHIPS BETWEEN RIPARIAN CANOPY VEGETATION AND SOILS IN THE OREGON COAST RANGE

Abstract

Source-sink relationships between plants and soils are species and nutrient dependent. Shifts in species composition may alter source-sink relationships and potentially impact the nutrient dynamics of an ecosystem. In the central Coast Range of Oregon, Douglas-fir- and red alder-dominated riparian areas provide a test system in which to study the effects of different source-sink relationships on nutrient cycling under different species. Foliage, litter, and soils at 10 riparian sites dominated by Douglas-fir or red alder were analyzed for $\delta^{15}N$, $\delta^{13}C$, and nutrient concentrations. Douglas-fir and red alder had opposite source-sink relationships with soil for N exchange: Douglas-fir was primarily a sink for soil N whereas red alder was a source of N to the soil due to its ability to fix atmospheric N. Douglas-fir sites demonstrated greater N status and lighter soil $\delta^{15}N$ closer to the stream, trends not found at red alder sites. Prior site occupancy by red alder along the stream may have contributed a legacy of greater N availability and lower soil $\delta^{15}N$ near the stream on Douglas-fir sites. Foliage $\delta^{15}N$, soil $\delta^{15}N$, and soil %N did not indicate a presence of marine N from anadromous salmonids at our riparian sites. $\delta^{13}C$ and $\delta^{15}N$ of foliage and soil suggested litter decomposition processes varied depending on the vegetation composition. Soils under Douglas-fir were generally more enriched in ^{13}C compared to red alder even when the $\delta^{13}C$ of foliage inputs were similar. Differences between soil and foliage $\delta^{15}N$ were greater for Douglas-fir than red alder. A shift in species composition from red alder-dominated to Douglas-fir-dominated riparian areas may alter source-sink relationships with soil N and litter decomposition processes that have important implications for ecosystem processes.

Introduction

The nature of source-sink relationships between plants and soil varies with both the species and the element being considered. For carbon (C), there is essentially a one-way flow from plants to soil, although the composition of C inputs depends on the type of vegetation. In the case of leaf litter as a C source, deciduous and coniferous tree species have different litter chemistries that influence their rates of decomposition (Prescott et al. 2000). Unlike carbon, nitrogen (N) cycles bi-directionally between most plants and soils. For N-fixing species, though, the flow of N from the plant to the soil is much greater than the flow from the soil to the plant resulting in a more unidirectional flow (Vitousek and Howarth 1991). Therefore, shifts in species composition by natural or management processes have the potential to impact the nutrient dynamics of a system.

In the Coast Range of western Oregon, Douglas-fir (*Pseudotsuga menziesii*) and red alder (*Alnus rubra*), two common canopy species (Spies et al. 2002), offer a test system in which to study the effects of different source-sink relationships on ecosystem nutrient cycling. Both species commonly occur near streams (Nierenberg and Hibbs 2000) and are of interest as managers consider converting red alder-dominated riparian areas to those dominated by large conifers. The impacts of this conversion are unclear. For example, red alder has been shown to increase N-cycling by contributing N-rich litter inputs to soils (Turner et al. 1976, Van Miegroet and Cole 1984, Binkley et al. 1992).

Naturally occurring stable isotopes can offer insight into nutrient cycling and the nature of source-sink relationships between species. For a nutrient, the isotopic composition of foliage reflects that of its source or sources (Shearer and Kohl 1986, Robinson 2001). In the case of N, plants that fix atmospheric N_2 have a fairly narrow range of $\delta^{15}N$, between –2.0‰ and 2.0‰ (Shearer and Kohl 1986) relative to a reference of atmospheric N_2 at 0.0‰. Plants that access soil N generally have a wider range of $\delta^{15}N$, from –8.0‰ to +10.0‰ (Peterson and Fry 1987), partly due to the spatial heterogeneity of the soil $\delta^{15}N$ source. For C, soil

organic matter $\delta^{13}C$ reflects the isotope signature of the C source, which can vary among plant species with different physiologies (Garten and Taylor 1992, Marshall and Zhang 1994) and photosynthetic pathways (Rounick and Winterbourn 1986) growing in the same environment. The variations in the $\delta^{13}C$ of plants arise from differential fractionation of the C isotope ratio during CO_2 fixation and constraints on diffusion by stomata (Ehleringer et al. 2000). These differences may be manifest in soil $\delta^{13}C$ and help describe the primary source of C inputs.

In addition to identifying source-sink relationships, stable isotopes can be used to describe nutrient inputs and nutrient cycling rates in a system. Patterns of $\delta^{15}N$ in plants and soils have been related to nitrification and/or mineralization rates (Garten 1993, Garten and Van Miegroet 1994, Koopmans et al. 1997, Emmett et al. 1998), level of mycorrhizal associations (Hobbie et al. 1999a, b, Hobbie et al. 2000, Hobbie and Colpaert 2003), the depth and form of N uptake (McKane et al. 2002) and inputs of marine derived N to riparian ecosystems (Ben-David et al. 1998, Helfield and Naiman 2002, Bilby et al. 2003, Reimchen et al. 2003). Stable isotopes of carbon have been used to track changes in vegetation composition for species using different photosynthetic pathways (Wedin et al. 1995), and improve understanding of litter decomposition (Wedin et al. 1995, Quideau et al. 2003) and soil organic matter turnover (Chen et al. 2002).

For this study, we used stable isotopes of N and C to investigate source-sink relationships between Douglas-fir, red alder, and soils and how both species moderate N dynamics and C inputs through leaf litter in riparian environments of the Oregon Coast Range. To do this, we selected 10 riparian sites dominated by either Douglas-fir or red alder and sampled foliage, litter, and soils at each site. Stable isotope compositions of N and C described differences between Douglas-fir- and red alder-dominated sites in N dynamics, N inputs, and C inputs.

Methods

Study area

The study was located in the central Coast Range of western Oregon in the Upper Alsea, Lake Creek, and Lower Siuslaw watersheds. The Coast Range formed during the tertiary period from uplifting of the ocean floor and is composed primarily of marine sandstones and basaltic volcanic rock (Orr et al. 1992). Soils are generally moderately deep sandy loams to clay loams with dark surface horizons high in organic matter (Franklin and Dyrness 1988). The maritime climate is moderate with warm, dry summers and cool wet winters. Rain is the predominant form of precipitation and falls mostly from October to March with average yearly rainfall of 150 to 300 cm. The study area falls in the western hemlock (*Tsuga heterophylla*) vegetation zone with major forest tree species of Douglas-fir, western hemlock, and western redcedar (*Thuja plicata*) (Franklin and Dyrness 1988). Red alder and bigleaf maple (*Acer macrophyllum*) are common hardwood species.

Study sites

Five riparian sites dominated by Douglas-fir and 5 dominated by red alder were selected for study in July of 2002 (Table 3.1). All sites were located within approximately 75 km of the Pacific Ocean with a north/south range of 80 km. Study sites were selected in 2^{nd}-4^{th} order streams with relatively unconstrained reaches and monospecific overstories. Red alder dominated the canopy on red alder sites with a few big leaf maple and/or conifers sometimes present. The canopy was generally closed, and tree age ranged from 30-60 years of age. Douglas-fir dominated the canopy of Douglas-fir sites with a few bigleaf maple, western hemlock, and western redcedar occasionally present. Most Douglas-fir sites had some red alder along the stream, but these were usually small, individual trees. No Douglas-fir site had a notable amount of upslope red alder. Tree age ranged from 40 to over 100 years old.

Table 3.1. Site characteristics

5th field watershed	Site	Riparian habitat	Average bankfull width (m)	Average dbh* of sampled trees (cm)	Parent material	Location	Elevation (m)
Upper Alsea River	Alsea tributary	Douglas-fir	1.4	59.0	sandstone	44° 19' N, 123° 28' W	284
	Yew Creek	Douglas-fir	3.4	46.6	basalt	44° 30'N, 123°33' W	240
	Trout Creek	Douglas-fir	4.3	106.9	basalt	44° 22' N, 123° 32'W	289
	South Fork of Alsea	Douglas-fir	1.2	45.8	basalt	44° 21'N, 123° 34'W	320
	Honey Grove	red alder	4.7	37.8	sandstone	44° 23' N, 123° 32' W	302
	Coleman Creek	red alder	7.0	27.1	sandstone	44° 18' N, 123° 30' W	287
	Record Creek	red alder	3.4	44.1	sandstone	44° 20' N, 123° 38' W	137
Lake Creek	Nelson Creek	red alder	6.7	43.2	sandstone	44° 36'N, 123° 36' W	165
Lower Siuslaw River	Wolf Creek	Douglas-fir	6.3	53.1	sandstone	43° 55'N, 123° 21' W	187
	Smith Creek	red alder	5.0	31.2	sandstone	43° 50' N, 123° 22'W	263

*dbh = diameter at breast height

Vegetation sampling

One plot was established at each of the ten sites (Figure 3.1). Each plot extended 20 m upland from the edge of the active channel and 50 m along the stream. Five trees of the dominant canopy species were sampled per plot for foliage in a cross pattern; 3 trees were sampled at roughly 10 m upslope from the stream at 0, 25, and 50 m from the down-stream edge of a plot, and two additional trees were sampled along the stream edge and 20 m from the stream. Foliage was collected with a shotgun from the middle-to-upper canopy of all trees. To insure similar light conditions, all foliage was collected from streamside branches. Approximately 50-70 first year needles from Douglas-fir and 5 fully expanded leaves from red alder were collected from each tree for a total of 5 foliage samples per site. Foliage from salmonberry (*Rubus spectabilis*), swordfern (*Polystichum munitum*), and vine maple (*Acer circinatum*) was collected at the midline of each plot from one shrub near the stream. Leaves collected were from the top of each plant.

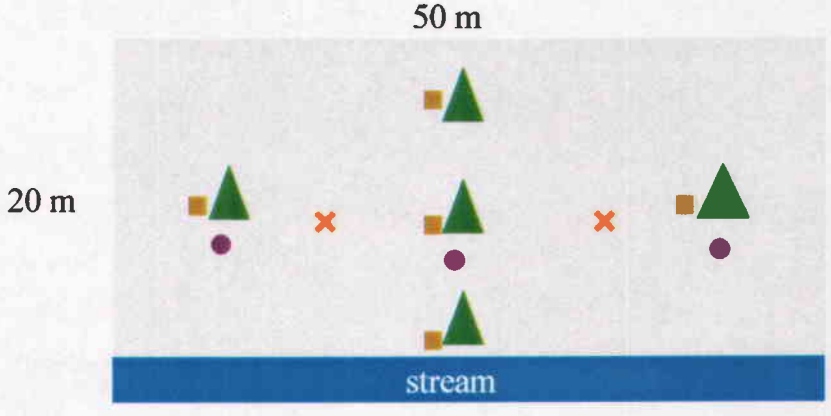

Figure 3.1. Plot schematic. Symbols represent foliage (▲), soil (■), litterfall (×), and forest floor (●) sampling positions.

Soil and litter sampling

Five composite samples of soil were collected with a 5 cm diameter corer from the upper 10 cm of mineral soil around the base of each tree that was sampled for foliage (see Table A.1. in the appendix for a more detailed description of soils). Three samples from the O_i horizon (termed "forest floor") were collected above the point where soil samples were taken under the three sampled trees at 10 m from the stream. Litterfall was collected at each plot in the fall of 2002 in both halves of each plot with two laundry baskets (60 x 45 cm) containing a suspended mesh net. Litterfall was collected from the baskets after one week.

Isotope and nutrient analysis

Foliage, forest floor, and litterfall were separately dried at 50° C for 48 hours and ground with mortar and pestle followed by a ball mill for 15-25 seconds to produce a fine powder. Soil was passed through a 2.36mm sieve to remove rocks and roots and then dried at 60° C for 72 hours and ground similarly to foliage. All equipment was wiped with acetone between each sample. Foliage, litter, leaf fall, and soil were analyzed on a continuous flow PDZ Europa Scientific 20/20 mass spectrometer at the Berkeley Center for Stable Isotope Biogeochemistry, University of California at Berkeley, for $\delta^{15}N$, %N, $\delta^{13}C$, and %C composition. Isotope values are expressed in delta notation (δ):

$$\delta X = [(R_{sample} / R_{standard}) - 1]\ 1000$$

where δX is the ratio of $^{15}N/^{14}N$ or $^{13}C/^{12}C$ compared to the international standards (atmospheric N_2 for nitrogen, Pee Dee Belemnite for C), R_{sample} is the ratio of the heavy to light isotope of the sample, and $R_{standard}$ is the ratio of the heavy to light isotope of the standard. The precision of isotope analysis for replicate samples was within 0.17‰ for $\delta^{15}N$ and 0.16‰ for $\delta^{13}C$. An enrichment factor (the difference between plant and soil $\delta^{15}N$; $\varepsilon = \delta^{15}N_{plant} - \delta^{15}N_{soil}$) was used to standardize differences between soil and foliage $\delta^{15}N$ across sites as described by Garten (1993) and Garten and Van Miegroet (1994).

Data analysis

Data were analyzed using linear regression to compare trends among $\delta^{15}N$, %N, enrichment factors, and distance from the stream on Douglas-fir- and red alder-dominated sites after accounting for correlations between trees on the same site (n = 5 for all comparisons). The estimate of the overall slope is a weighted average of the regression coefficients of the response variable on the independent variable estimated separately for each of the five sites. All models had two main effects, with "site" as one of those main effects in each comparison. No interaction term between main effects was tested because we were not interested in patterns on individual sites, only overall site trends. Mean soil $\delta^{13}C$ and foliage $\delta^{13}C$ were compared separately between Douglas-fir and red alder sites with t-tests (n = 10). Similar tests were run for mean soil $\delta^{15}N$ and mean foliage $\delta^{15}N$. Significance levels were set at ≤ 0.05 prior to the analysis. All statistical procedures were conducted using statistical software from the SAS Institute Inc. (SAS 1999).

Results

$\delta^{15}N$ patterns in foliage types and soils

Douglas-fir demonstrated greater $\delta^{15}N$ variability in foliage stages (i.e. green foliage, litterfall, and forest floor) compared to red alder across sites (Figure 3.2). At the level of individual trees, Douglas-fir foliage $\delta^{15}N$ ranged from almost -4.0‰ to 0.2‰ while red alder foliage $\delta^{15}N$ was between -1.5‰ to -0.5‰ (Figure 3.3). Douglas-fir foliage $\delta^{15}N$ was generally depleted relative to red alder foliage $\delta^{15}N$ when site means were compared (Figure 3.4a; t-test, t = -2.30, p = 0.05 with 8 degrees of freedom, n = 10). Litterfall and forest floor had similar ranges in $\delta^{15}N$ to that of foliage $\delta^{15}N$ for each species (Figure 3.2). The sample average $\delta^{15}N$ for Douglas-fir litterfall and forest floor were between -3.0‰ and -1.0‰ while the range of sample average $\delta^{15}N$ for red alder litterfall and forest floor was less, between –1.6‰ and –1.0‰. Foliage stages were depleted relative to mineral

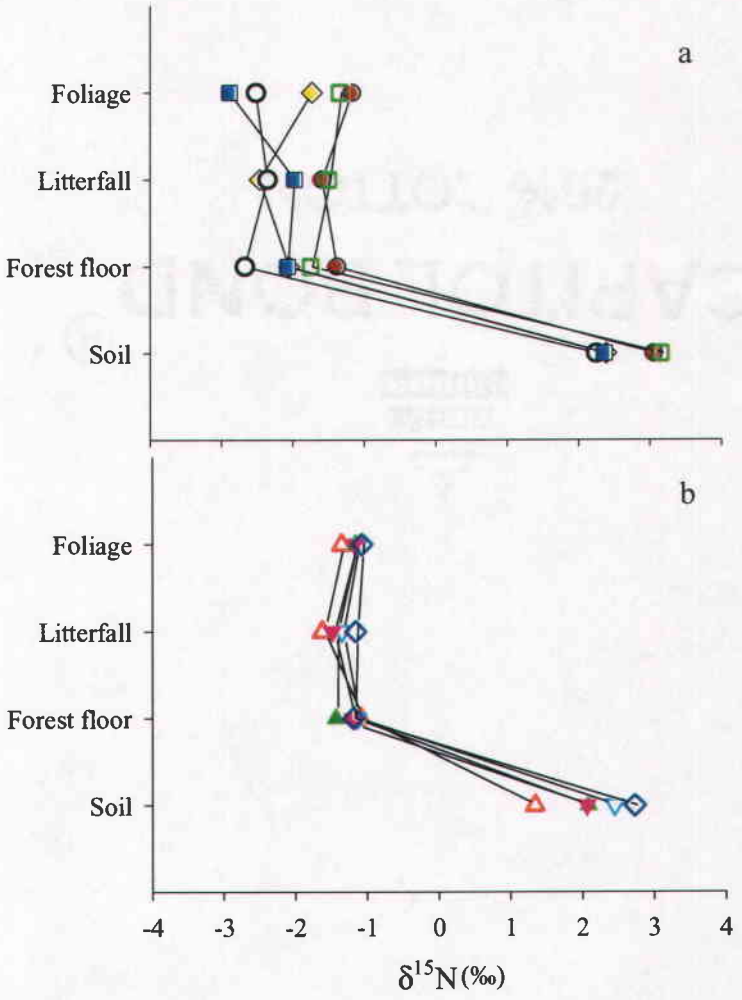

Figure 3.2. The average $\delta^{15}N$ among Douglas-fir (a) and red alder (b) foliage (n = 5), litterfall (n = 2), forest floor (n = 3; "foliage stages"), and soils for each site. Douglas-fir sites are Alsea (◆), Trout (●), Wolf (○), South Fork (□), Yew (■). Red alder sites are Coleman (△), Nelson (▲), Honey Grove (▽), Smith (▼), Record (◇).

soil at all sites by on average 3.4‰ for red alder and 4.6‰ for Douglas-fir (Figure 3.2). There were no significant differences between Douglas-fir and red alder in soil $\delta^{15}N$.

Measures of N status across sites

Foliage $\delta^{15}N$, foliage %N, soil $\delta^{15}N$, and enrichment factors were significantly related with distance away from the stream at Douglas-fir sites (Table 3.2). $\delta^{15}N$ and nitrogen concentration (%N) of Douglas-fir needles were greatest near the stream (Figures 3.3a, 3.5). Soil $\delta^{15}N$ was positively related to distance from the stream (Figure 3.6a). Soil %N and soil C:N ratios had significant relationships with soil $\delta^{15}N$, lighter soil $\delta^{15}N$ occurred where soil %N was higher and the C:N was lower (Table 3.2, Figure 3.6). Enrichment factors ($\varepsilon_{plant\text{-}soil}$) for Douglas-fir sites approached zero closer to the stream and were significantly related to foliage %N (Figure 3.7, Table 3.2). Needle $\delta^{15}N$ was not associated with soil $\delta^{15}N$ or soil %N (data not shown). There was no significant association of distance away from the stream on soil %N (Table 3.2, Figure 3.8a).

Red alder did not demonstrate the patterns of $\delta^{15}N$ and N status we found at Douglas-fir sites. There was no significant relationship between distance away from the stream and foliage $\delta^{15}N$, foliage %N, soil %N, soil $\delta^{15}N$, and enrichment factors at red alder sites (Table 3.2, Figures 3.2b, 3.8b, 3.9). All but one soil sample had a C:N below 30 indicating generally high N availability at all sites. Although the effect of soil $\delta^{15}N$ on foliage $\delta^{15}N$ was non-significant, the highest foliage $\delta^{15}N$ values occurred at high soil $\delta^{15}N$ and the lowest foliage $\delta^{15}N$ occurred at low soil $\delta^{15}N$.

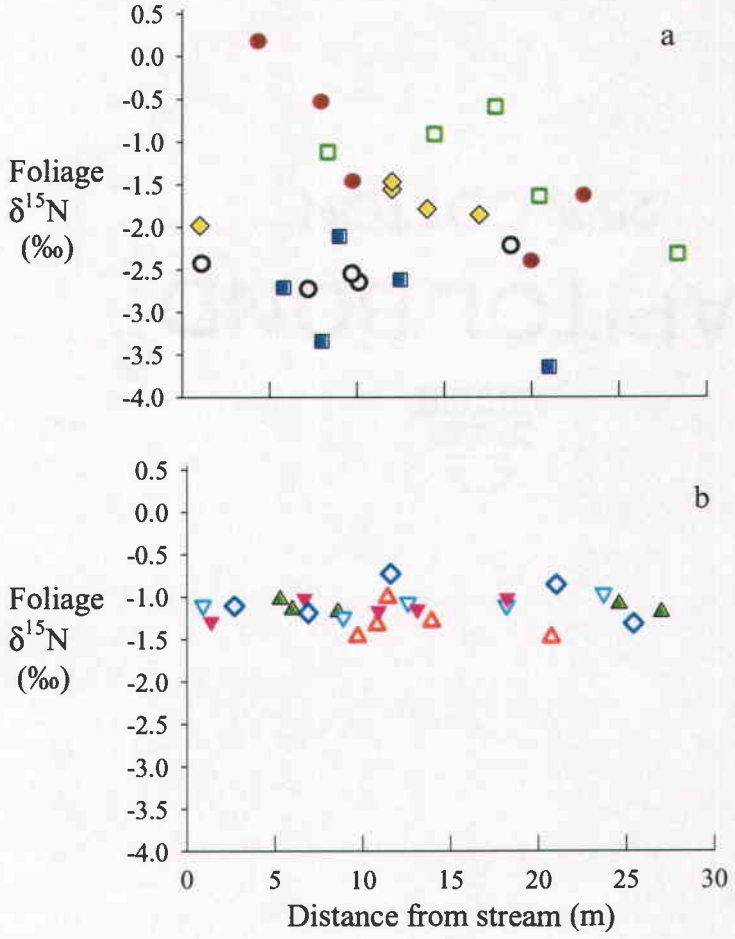

Figure 3.3. The foliage $\delta^{15}N$ of Douglas-fir (a) and red alder (b) with distance from the stream. Symbols as in Figure 3.2.

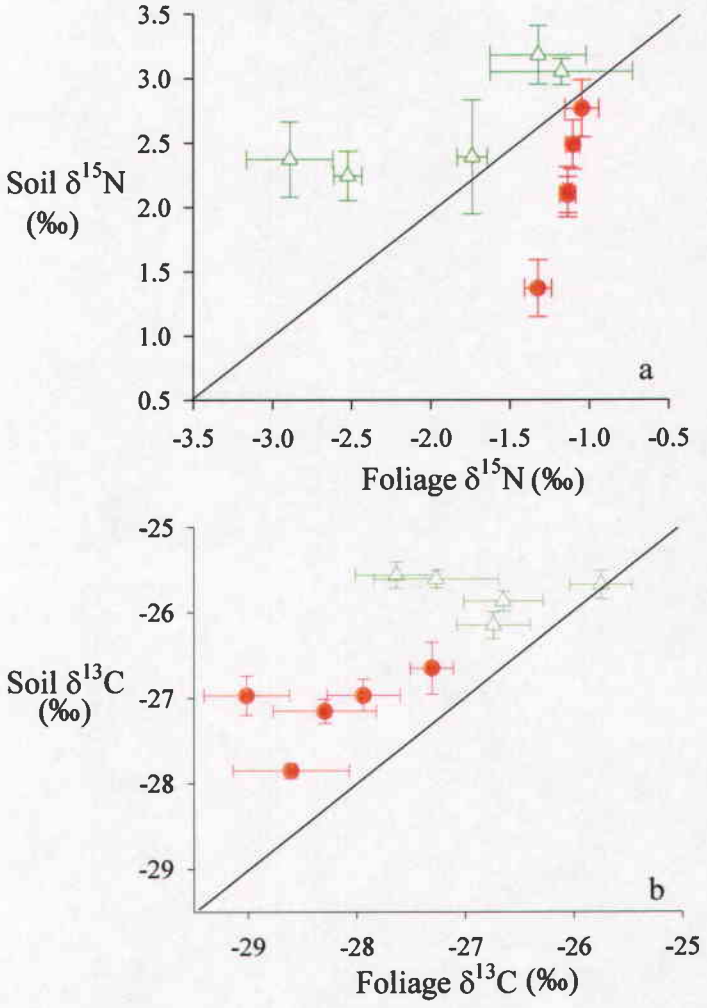

Figure 3.4. The relationship between average (+/- 1 standard error) soil and foliage $\delta^{15}N$ (a) and $\delta^{13}C$ (b) for red alder (●) and Douglas-fir (▲). Included are the lines: (a) $y = x+4$, (b) $y = x$.

Table 3.2. Linear regression results for riparian variables after accounting for within site correlations between trees. The estimate is a weighted average of the regression coefficients of the response variable (i.e. foliage %N) on the independent variable (i.e. DFS) estimated separately for each of the five sites. The significance level was set at p = 0.05 prior to the analysis. DFS = distance from stream. N = 5 for all comparisons.

Douglas-fir	Estimate (std error)	Confidence limits for estimate	p-value
foliage %N v. DFS	***-0.006 (0.003)***	***-0.011, 0.000***	***0.05***
foliage $\delta^{15}N$ v. DFS	***-0.049 (0.018)***	***-0.861, -0.012***	***0.01***
soil $\delta^{15}N$ v. DFS	***0.053 (0.017)***	***0.018, 0.089***	***0.005***
$\varepsilon_{plant\text{-}soil}$ v. DFS	***-0.103 (0.021)***	***-0.146, -0.059***	***<0.001***
soil $\delta^{15}N$ v. Soil %N	***-4.746 (1.166)***	***-7.186, -2.305***	***<0.001***
soil $\delta^{15}N$ v. Soil C:N	***0.030 (0.008)***	***0.013, 0.047***	***0.002***
foliage $\delta^{15}N$ v. Soil %N	-1.202 (1.585)	-4.519, 2.114	0.457
soil %N v. DFS	-0.001 (0.003)	-0.007, 0.005	0.784
foliage $\delta^{15}N$ v. soil $\delta^{15}N$	-0.125 (0.230)	-0.605, 0.356	0.594
$\varepsilon_{plant\text{-}soil}$ v. foliage %N	***5.171 (2.085)***	***0.806, 9.536***	***0.023***
Red alder			
folaige %N v DFS	-0.006 (0.006)	-0.018, 0.006	0.286
foliage $\delta^{15}N$ v. DFS	0.001 (0.004)	-0.009, 0.010	0.898
soil $\delta^{15}N$ v. DFS	0.021 (0.011)	-0.003, 0.045	0.077
$\varepsilon_{plant\text{-}soil}$ v. DFS	-0.021 (0.012)	-0.046, 0.005	0.107
soil %N v. DFS	0.005 (0.003)	-0.002, 0.012	0.128
foliage $\delta^{15}N$ v. soil $\delta^{15}N$	-0.001 (0.082)	-0.172, 0.171	0.994

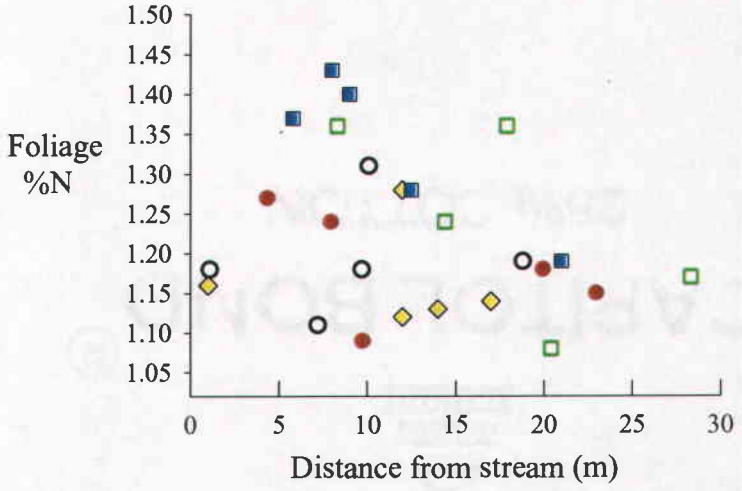

Figure 3.5. The relationship between foliage %N and distance from the stream for Douglas-fir sites. Symbols as in Figure 3.2.

Foliage and soil $\delta^{13}C$

Douglas-fir foliage was more enriched in ^{13}C than red alder when individual site means for $\delta^{13}C$ were compared (t-test, $t = 3.30$, $p = 0.01$ with 8 degrees of freedom, $n = 10$; Figure 3.4b). Average $\delta^{13}C$ of Douglas-fir soil was also significantly more enriched in ^{13}C than red alder soil when site means were compared (t-test, $t = 5.91$, $p < 0.001$ with 8 degrees of freedom, $n = 10$). Generally, soil $\delta^{13}C$ was more enriched in ^{13}C than foliage $\delta^{13}C$ for Douglas-fir and red alder sites (Figure 3.4b). The average $\varepsilon_{plant\text{-}soil}$ for Douglas-fir and red alder was near 1.0‰.

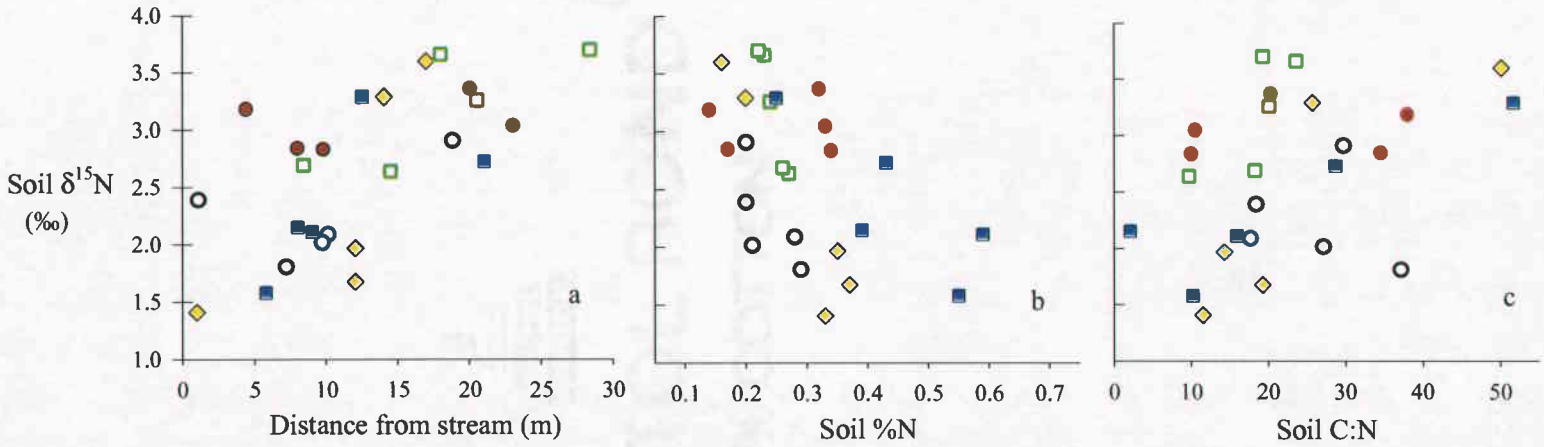

Figure 3.6. The relationship between soil $\delta^{15}N$ and distance from stream (a), soil %N (b), and soil C:N (c) for Douglas-fir sites. Symbols as in Figure 3.2.

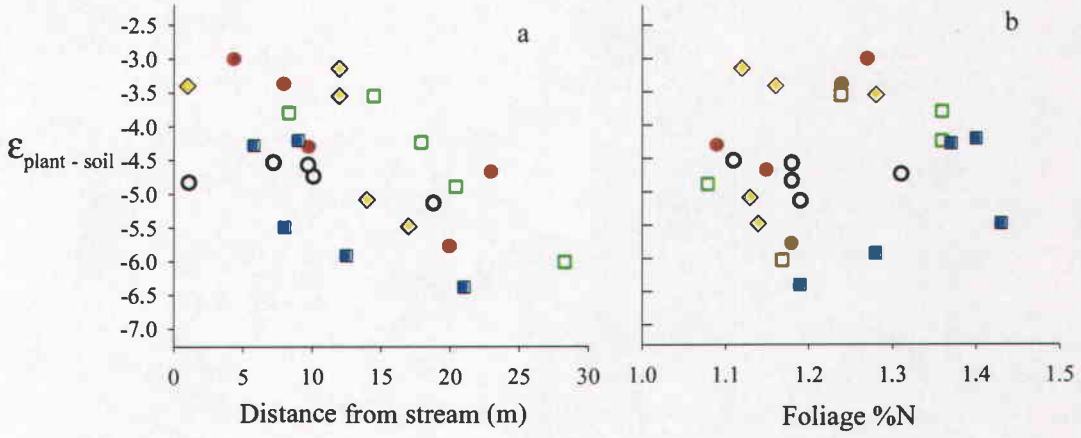

Figure 3.7. The relationship between enrichment factors and distance from the stream (a) and foliage %N (b) for Douglas-fir sites. Symbols as in Figure 3.2.

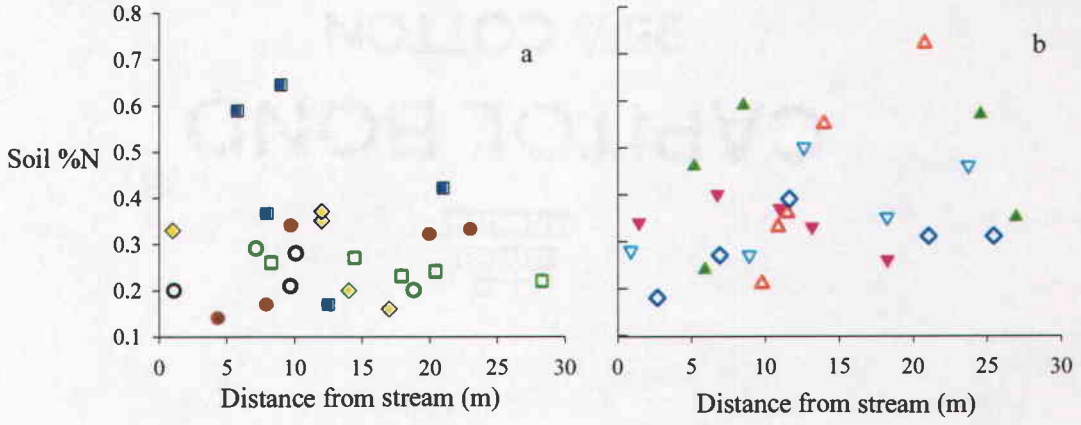

Figure 3.8. The relationship between distance from stream and soil %N for Douglas-fir (a) and red alder (b) trees. Symbols as in Figure 3.2. Neither species demonstrated a statistically significant relationship between distance from stream and soil %N.

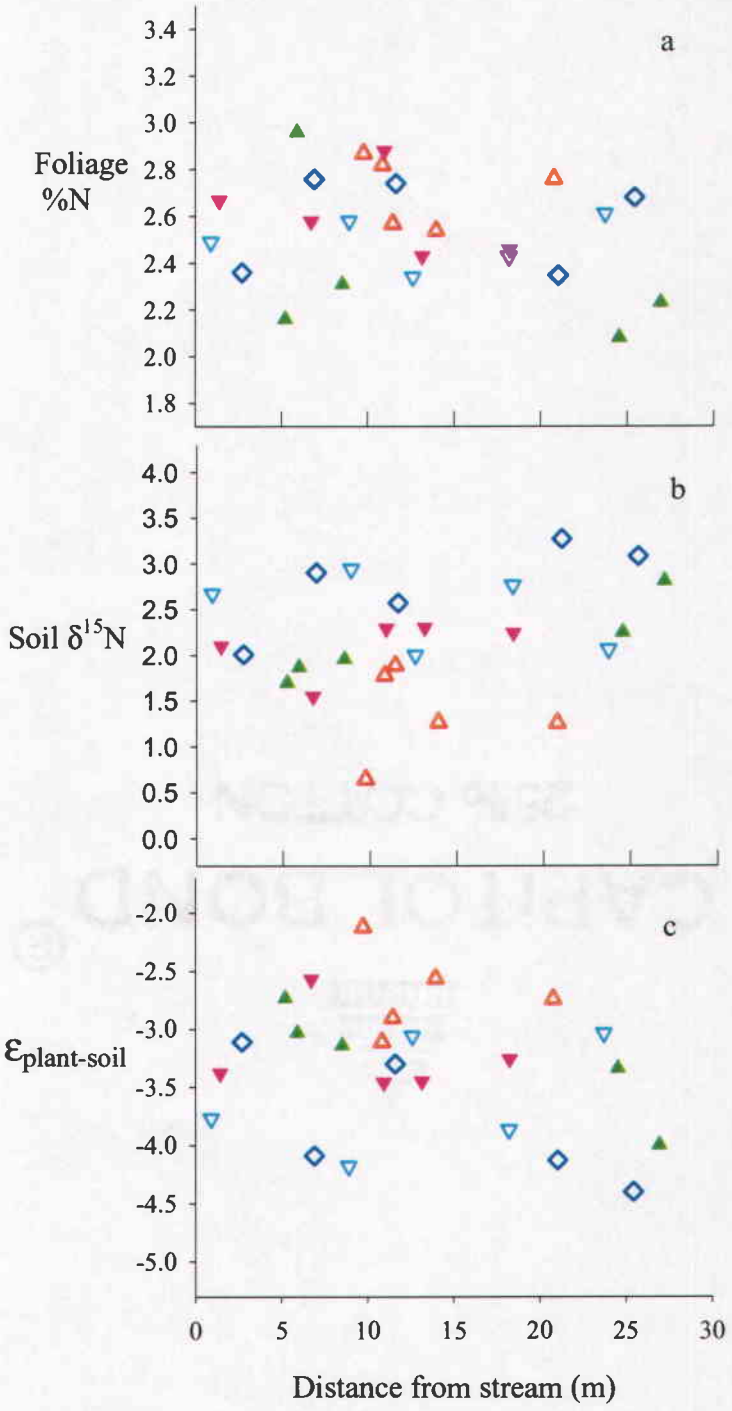

Figure 3.9. The relationship between foliage %N (a), soil $\delta^{15}N$ (b), and enrichment factors (c) with distance from the stream on red alder sites. Symbols as in Figure 3.2.

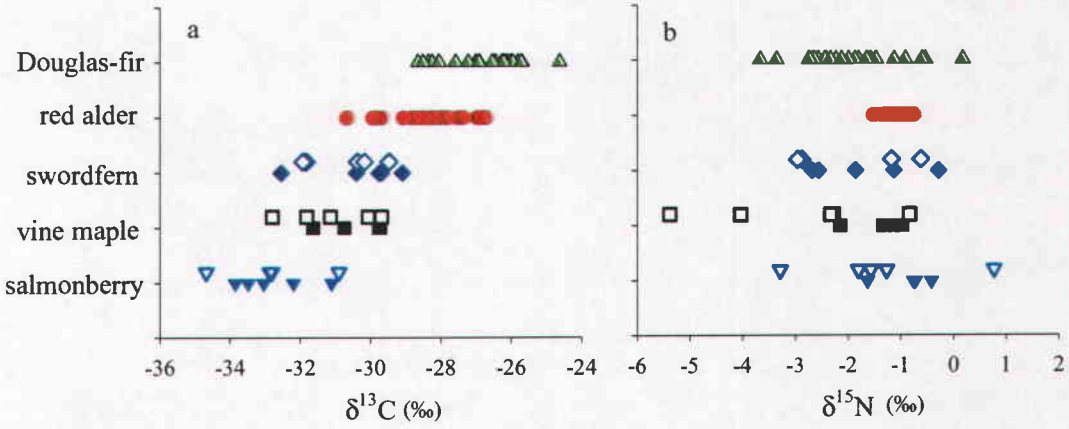

Figure 3.10. The $\delta^{13}C$ (a) and $\delta^{15}N$ (b) of Douglas-fir, red alder, swordfern, vine maple, and salmonberry from all sites. Points are individual samples. For understory vegetation, open shapes denote Douglas-fir-dominated sites; closed shapes are red alder-dominated sites.

Understory

Understory vegetation (vine maple, salmonberry, and swordfern) was generally more depleted in ^{13}C than Douglas-fir and red alder (Figure 3.10a). All $\delta^{13}C$ of the understory were less than -29.0‰ for all species with the lowest $\delta^{13}C$ roughly -34.5‰. Salmonberry was generally depleted in ^{13}C while vine maple and swordfern had similar ranges of $\delta^{13}C$. Understory species were similar in $\delta^{15}N$ to Douglas-fir and red alder, although the range of vine maple $\delta^{15}N$ was more negative than either canopy species (Figure 3.10b).

Discussion

N source and sink relationships

Patterns of $\delta^{15}N$ at Douglas-fir and red alder sites suggested opposite source-sink relationships with soil for N exchange. The variation in foliage $\delta^{15}N$ of

Douglas-fir suggested soil was its primary source of N and hence was a sink for soil N; red alder's ability to fix atmospheric N_2 (Bormann et al. 1994) decreased its reliance on soil for N which suggested it was a net source of N to the soil.

Foliage $\delta^{15}N$ of non-N_2-fixing plants, like Douglas-fir, can be influenced by multiple processes (Robinson 2001, Evans 2001), so it is not surprising there was no relationship between foliage and soil $\delta^{15}N$ (Table 3.2). The integration of multiple soil N pools that were spatially and temporally heterogeneous in $\delta^{15}N$ (Högberg 1997, Bundt et al. 2001) could cause the variation of almost 4.0‰ in foliage $\delta^{15}N$ among Douglas-fir sites (Figure 3.3a). Also, the uptake of different forms of soil N (i.e. NH_4 vs. NO_3; Högberg 1997, Evans 2001) and subsequent fractionation in $\delta^{15}N$ during the conversion of those N compounds to usable forms (Robinson 2001) can also contribute to the large variation in foliage $\delta^{15}N$.

Conversely, the low variability of red alder foliage $\delta^{15}N$ suggested it had little dependence on soil N and fixed most of its N from the atmosphere. Red alder foliage $\delta^{15}N$ was always between –1.0‰ to –1.5‰ (Figure 3.3b), values common for N_2-fixing species (Shearer and Kohl 1986) and similar to other alder grown in N-free media (Binkley et al. 1985, Hurd et al. 2001). Also, there was little variation in foliage $\delta^{15}N$ among trees across all sites, which suggests red alder was accessing a spatially homogenous N source, the atmosphere. Atmospheric N_2 has a constant $\delta^{15}N$ of 0.0‰ (Shearer and Kohl 1986) that, coupled with little fractionation during fixation (Kohl and Shearer 1980, Högberg 1997), results in foliage $\delta^{15}N$ of a value similar to the atmosphere when N_2-fixing rates are high (Shearer and Kohl 1986).

The effect of soil N availability on the rate of N_2-fixation in red alder is unclear. Theory predicts that N_2-fixation will decrease when the resource cost of fixation exceeds that of acquiring N through other means, such as from the soil (Vitousek et al. 2002). However, previous studies have produced conflicting evidence on whether N_2-fixation in red alder decreases when soil N is readily available (reviewed by Binkley et al. 1994). Although we did not measure the rate

of fixation by red alder, the narrow range of foliage $\delta^{15}N$ for the red alder we sampled implied these trees were fixing most of their N even though soil %N was high (Figures 3.3b, 3.8b). Other environmental factors besides the availability of soil N may influence the rate of N_2-fixation in red alder.

Despite different levels of dependence on soil for N, Douglas-fir and red alder foliage $\delta^{15}N$ through all stages were always lighter than soil $\delta^{15}N$ (Figure 3.2). This difference can be developed by any of several mechanisms. First, decomposition discriminates against the heavier isotope leaving soils relatively more enriched in ^{15}N compared to vegetation (Nadelhoffer and Fry 1988). Second, nitrification, ammonification, and denitrification all fractionate against ^{15}N, leaving soils enriched in the heavier isotope (Högberg 1997, Hedin et al. 1998). Finally, mycorrhizal transfer of N to plants fractionates against ^{15}N, particularly at low N availability, resulting in lighter vegetation isotope ratios compared to soils for non-N-fixing species (Hobbie et al. 1999b, Hobbie and Colpaert 2003).

Virtually all studies comparing vegetation and soils have also found foliage stages to be consistently more depleted in ^{15}N than soils (Garten 1993, Garten and Van Miegroet 1994, Koopmans et al. 1997, Emmett et al. 1998, Vogel and Gower 1998), although Binkely et al. (1985) found the opposite between Douglas-fir needles and soils at two sites in the Pacific Northwest. It is not clear what caused this observation, but their foliage $\delta^{15}N$ was notably higher than any value we found (> 7.0‰ for Binkley et al. (1992) versus 0.2‰ for and our data).

Spatial patterns of N status

Our data suggest Douglas-fir sites had higher N status near the stream compared to upslope that influenced foliage and soil $\delta^{15}N$. First, foliage %N, as a proxy for N availability (Prescott et al. 2000, Hobbie and Colpaert 2003), had the highest values close to the stream (Figure 3.5). Second, soil $\delta^{15}N$ was related to distance from the stream and two measures of soil N status: soil %N, and soil C:N ratios (Figure 3.6). Soil %N was high and C:N ratios were low where soil $\delta^{15}N$ was

relatively depleted in ^{15}N, near to the stream, indirectly suggesting N was more available close to the stream. Third, enrichment factors ($\varepsilon = \delta^{15}N_{foliage} - \delta^{15}N_{soil}$) were closer to zero near the stream (Figure 3.7a). The mechanism(s) behind the N gradient and its subsequent influence on $\delta^{15}N$ is not clear because our soil $\delta^{15}N$ data contradicts expected patterns based on previous work using $\delta^{15}N$ to assess the rate of N cycling at a site (Garten 1993, Garten and Van Miegroet 1994, Koopmans et al. 1997, Emmett et al. 1998, Pardo et al. 2002, Koba et al. 2003). Where N cycles rapidly, soils become more positive in $\delta^{15}N$ due losses of the isotopically light N through leaching and denitrification (Nadelhoffer and Fry 1988, Högberg 1997, Hedin et al. 1998). Subsequently, plants become enriched in ^{15}N as they take up heavier soil N sources and become more similar to soil $\delta^{15}N$, resulting in enrichment factors closer to zero (Garten and Van Miegroet 1994). Although our enrichment factors also follow this pattern by becoming closer to zero where the N status was higher, soil $\delta^{15}N$ becomes more negative, the opposite of what would be expected (Garten and Van Miegroet 1994, Högberg 1997; Figure 3.6a). Although different rates of N cycling processes are likely influencing the N gradient at our sites, they are clearly not the only factors influencing $\delta^{15}N$.

Hobbie et al. (1999a, b, 2000) and Hobbie and Colpaert (2003) have suggested soil and foliage $\delta^{15}N$ at different levels of soil N indicate the level of mycorrhizal association, rather than N-cycling processes. High soil N allows more direct N acquisition by plants from soils, whereas low soil N increases the reliance of non-N-fixing plants on mycorrhizae for N. Large fractionation during N transfer through fungal symbionts depletes foliage in ^{15}N and increases the difference in $\delta^{15}N$ between plants and soils where N is limited (Hobbie et al. 1999b, Hobbie et al. 2001, Hobbie and Colpaert 2003). At our Douglas-fir sites, enrichment factors suggested mycorrhizal relationships with Douglas-fir might better describe our $\delta^{15}N$ patterns versus N-cycling processes. First, the difference between foliage and soil $\delta^{15}N$ (ε) was smaller where the N status was relatively high, along the stream (Figure 3.7a). Second, enrichment factors were closer to zero at high foliage %N

(Figure 3.7b). These findings suggest the relatively high N environment near the stream reduced the reliance of streamside Douglas-fir on mycorrhizae for N compared with upslope trees. Further study analyzing the level of mycorrhizal infections of Douglas-fir with distance from the stream would add greater strength to this conclusion.

Influence of anadromous salmonids in riparian areas

In the Pacific Northwest, marine-derived nitrogen from spawning salmon can influence soil and vegetation $\delta^{15}N$ in riparian ecosystems (Ben-David et al. 1998, Helfield and Naiman 2002, Bilby et al. 2003, Reimchen et al. 2003). Salmon are isotopically heavy (>10.0‰, Bilby et al. 1996) and can enrich soils, vegetation and other organisms in ^{15}N, particularly near stream areas (Bilby et al. 1996, Ben-David et al. 1998, Reimchen et al. 2003). The Oregon Coast Range has several species of anadromous salmonids that have the potential to contribute marine nutrients, including N, to riparian ecosystems (Reeves et al. 2002). Added N inputs from salmon carcasses and feces from piscivorous animals feeding on the carcasses increase N availability (Bilby et al. 2003) and may stimulate N cycling, both of which can influence soil and vegetation $\delta^{15}N$.

Although several species of Pacific salmon (*Oncorhynchus kisutch, O. mykiss, O. tshawytscha*) have been documented at most of our sites (Oregon Dept. of Fish and Wildlife, http://rainbow.dfw.state.or.us/nrimp/information/index), it is unlikely they were a strong influence on N availability or $\delta^{15}N$. First, the $\delta^{15}N$ and %N of soil and foliage at our sites with barriers to anadromy (Alsea and Coleman Creeks) were similar to the other sites without barriers. Second, neither foliage $\delta^{15}N$, soil $\delta^{15}N$, nor soil %N were more enriched in ^{15}N closer to the stream to suggest marine N contributions at either Douglas-fir or red alder sites (Figures 3.3, 3.6a, 3.8, 3.9b; Ben-David et al. 1998, Reimchen et al. 2003). Instead, soil $\delta^{15}N$ at Douglas-fir sites demonstrated the opposite trend while soil and foliage $\delta^{15}N$ at red alder sites had no spatial pattern (Figures 3.3b, 3.6a, 3.9b). Although Douglas-fir

foliage $\delta^{15}N$ was more enriched in ^{15}N near the stream relative to upslope, needle $\delta^{15}N$ was lighter than foliage $\delta^{15}N$ of other studies where salmon were spawning (Ben-David et al. 1998, Helfield and Naiman 2002, Reimchen et al. 2003). It is possible our plot was not deep enough to escape an overall marine influence on $\delta^{15}N$ in riparian areas versus upslope, but the increase in Douglas-fir soil $\delta^{15}N$ of almost 2.0‰ from stream bank to 30 m from the stream does not suggest that this was likely. Reimchen et al. (2003) were able to detect a decrease in marine influences on $\delta^{15}N$ in wood samples from western hemlock at spawning sites within 10 m of the stream. At red alder sites, marine N may be less important as a N source where N inputs from red alder litter are available (Helfield and Naiman 2002). Helfield and Naiman (2002) found the importance of marine N as a N source for vegetation was reduced at spawning sites in Alaska when alder (*Alnus crispa*) was present.

The role of red alder in riparian areas

Red alder's ability to contribute large amounts of fixed N to soils may influence the soil $\delta^{15}N$ gradient found at Douglas-fir sites. Red alder is common in Oregon Coast Range riparian areas, particularly near streams (Pabst and Spies 1999, Nierenberg and Hibbs 2000), and produces large quantities of N-rich litter (Bormann et al. 1994). The litterfall and forest floor $\delta^{15}N$ of red alder changed little from that of foliage (Figure 3.2b) resulting in inputs of uniform $\delta^{15}N$ to the soil that could "flood" soil $\delta^{15}N$ with the red alder isotope signature. Changes in soil total $\delta^{15}N$ occur slowly over time (Johannisson and Högberg 1994, Högberg 1997), but red alder's presence in the Oregon Coast Range for thousands of years (Spies et al. 2002), with annual litter inputs of constant $\delta^{15}N$, suggests the influence of red alder on total soil $\delta^{15}N$ is potentially high. Also, the temporal stability of total soil $\delta^{15}N$ could allow red alder $\delta^{15}N$ to persist in riparian soils even after red alder is gone (Johannisson and Högberg 1994). Surprisingly, though, soil $\delta^{15}N$ at red alder sites was slightly more variable than that of Douglas-fir sites (Figure 3.2).

The history of our red alder sites, such as past vegetation composition or disturbances such as floods, could influence soil $\delta^{15}N$ prior to red alder colonization to create different initial soil $\delta^{15}N$. In time, the continued presence of red alder on these sites may drive soil $\delta^{15}N$ to a common value.

The ability of red alder to control soil N (Luken and Fonda 1983, Binkley et al. 1992) combined with the common spatial pattern of decreased red alder density away from streams (Pabst and Spies 1999, Nierenberg and Hibbs 2002) could explain the N availability gradient and $\delta^{15}N$ patterns found at our Douglas-fir sites as well as the lack of any similar relationship at red alder sites. Douglas-fir soil $\delta^{15}N$ close to the stream was near 2.0‰, similar to the average soil $\delta^{15}N$ across red alder sites (average 2.2‰; Figures 3.6a, 3.9b). The past occurrence of red alder along the stream on Douglas-fir sites may have decreased soil $\delta^{15}N$ relative to upslope soils over time, despite nitrifying and denitrifying processes that fractionate against the heavier isotope. The legacy effect of total soil $\delta^{15}N$ and the few streamside red alder present on some Douglas-fir sites may have perpetuated the red alder $\delta^{15}N$ influence on soil and explain the similarity in total soil $\delta^{15}N$ near the stream between Douglas-fir- and red alder-dominated sites. Although we did not find a significant relationship between Douglas-fir soil %N and distance away from the stream, overall soil %N was high and similar to that of red alder-dominated sites (Figure 3.8).

It is possible our samples did not capture the active soil N pools that Douglas-fir was accessing (Johannisson and Högberg 1994, Högberg 1997). This similarly explains the lack of relationship between Douglas-fir foliage $\delta^{15}N$ and soil $\delta^{15}N$ (Table 3.2). Active N pools have likely "lost" the red alder signature with rapid N cycling and may better reflect the $\delta^{15}N$ occurring from N cycling processes (i.e. nitrification, denitrification). Douglas-fir foliage $\delta^{15}N$ likely integrates short-term changes in soil $\delta^{15}N$ of active pools (Johannisson and Högberg 1994) as well

as the longer-term total soil $\delta^{15}N$ so that foliage and soil $\delta^{15}N$ are not directly related (Högberg 1997).

Decomposition

The $\delta^{13}C$ and $\delta^{15}N$ of soil and foliage suggested litter decomposition processes varied depending on the vegetation composition of the litter inputs. Despite some overlap in foliage $\delta^{13}C$ between Douglas-fir and red alder, soils under Douglas-fir were generally more enriched in ^{13}C compared to red alder (Figure 3.4b). Also, the difference between soil and foliage $\delta^{15}N$ was greater for Douglas-fir than for red alder (Figures 3.2, 3.4a). Differences in the chemical make-up of foliage between the species could influence decomposition processes (Prescott et al. 2000, Prescott 2002, Quideau et al. 2003) and be responsible for the generally higher $\delta^{13}C$ of Douglas-fir soils and greater difference between Douglas-fir foliage and soil $\delta^{15}N$ compared to red alder. For example, high N environments, such as those under N_2-fixing species like red alder, can decrease the rate of litter decomposition in later stages and lead to C accumulation in soil organic matter (Bormann et al. 1994, Carreiro et al. 2000, Michel and Matzner 2002, Resh et al. 2002, Saiya-Cork et al. 2002). One explanation for decreased decomposition is the reduced activity of fungal lignolytic enzymes under high N inputs (Carreiro et al. 2000, Saiya-Cork et al. 2002). Greater lignin accumulation, which is depleted in ^{13}C relative to bulk plant tissue (Wedin et al. 1995), would decrease the $\delta^{13}C$ of soil organic matter and may partly explain the lower $\delta^{13}C$ of red alder soils relative to Douglas-fir soils at our sites.

As demonstrated by other studies (Nadelhoffer and Fry 1988, Balesdent et al. 1993, Ehleringer et al. 2000, Chen et al. 2002), soils were generally more enriched in ^{13}C compared to vegetation (Figure 3.4b). In a few cases, soil $\delta^{13}C$ was lighter than the corresponding foliage samples at both red alder and Douglas-fir sites (data not shown). It is not clear what caused these soils to have lighter $\delta^{13}C$ than foliage, but inputs from understory vegetation is one possibility. Vine maple,

salmonberry, and swordfern were generally more depleted in ^{13}C than red alder and Douglas-fir foliage, sometimes by almost 4.0‰ (Figure 3.10a). The soil samples lighter than canopy foliage may reflect a stronger influence of this understory vegetation located above the sampling location.

The $\delta^{15}N$ of understory vegetation was similar to that of Douglas-fir and red alder and overlapped the overstory range of foliage $\delta^{15}N$ (Figures 3.4a, 3.10b). Although understory $\delta^{15}N$ could have also played a role in influencing soil $\delta^{15}N$, our data are not able to distinguish between canopy and understory foliage contributions to the soil.

Conclusions

Red alder and Douglas-fir demonstrated different source-sink relationships with soil N that have important implications for ecosystem processes. Douglas-fir and red alder both require N for growth and maintenance (and hence are transient N sinks), but the ability of red alder to fix N from the atmosphere also makes it an important N source for ecosystems. The added N from red alder can increase N-cycling making N more available for other riparian organisms (Helfield and Naiman 2002, Volk et al. 2003). Because Douglas-fir must remove N from the soil in order to fulfill its own N requirements, it does not have the same ability to contribute N to soils as red alder.

Current models of N cycling and N status in ecosystems using foliage and soil $\delta^{15}N$ (Garten 1993, Garten and Van Miegroet 1994, Koba et al. 2003) were not applicable in our system due to the ability of red alder to control the N dynamics and $\delta^{15}N$ of riparian soils. The current models of N-cycling found enriched soils in ^{15}N where N was cycling faster, which was opposite of what we found at Douglas-fir sites. Although red alder litter can increase the rates of N-cycling (Turner et al. 1976, Van Miegroet and Cole 1984, Binkley et al. 1992), the high influx of litter with a constant $\delta^{15}N$ near –1.5‰ may have served to keep soil $\delta^{15}N$ low. It is possible N-cycling processes such as nitrification and denitrification are still

enriching soils in ^{15}N where red alder is present (which may help account for the 3.0‰ to 4.0‰ enrichment in ^{15}N of soil compared to red alder foliage), but soils under red alder remained depleted in ^{15}N relative to most areas currently dominated by Douglas-fir. Measurements of nitrate leaching and denitrification rates in these soils may provide further insight into the N-dynamics of soils in these riparian areas. When evaluating N dynamics with isotope methods, species composition should be taken into account as potentially influencing the $\delta^{15}N$ patterns, especially when N-fixing species are present.

References

Balesdent, J., C. Girardin, and A. Mariotti. 1993. Site-related $\delta^{13}C$ of tree leaves and soil organic matter in a temperate forest. Ecology 74: 1713-1721.

Ben-David, M., T.A. Hanley, and D.M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. Oikos 83: 47-55.

Bilby, R.E., E.W. Beach, B.R. Fransen, J.K. Walter, and P.A. Bisson. 2003. Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. Transactions of American Fisheries Society 132: 733-745.

Bilby, R.E., B.R. Fransen, and P.A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53: 164-173.

Binkley, D., K. Cromack, Jr., and D.D. Baker. 1994. Nitrogen fixation by red alder: biology, rates, and controls. Pages 57-72 *in* D.E. Hibbs, D.S. DeBell, and R.F. Tarrant, editors. The biology and management of red alder. Oregon State University Press, Corvallis, OR.

Binkley, D., P. Sollins, and W.B. McGill. 1985. Natural abundance of nitrogen-15 as a tool for tracking alder-fixed nitrogen. Soil Science Society of America Journal 49: 444-447.

Binkley, D., P. Sollins, R. Bell, D. Sachs, and D. Myrold. 1992. Biogeochemistry of adjacent conifer and alder-conifer stands. Ecology 73: 2022-2033.

Bormann, B.T., K. Cormack, Jr., and W.O. Russell III. 1994. Influences of red alder on soils and long-term ecosystem productivity. Pages 47-56 *in* D.E. Hibbs, D.S. DeBell, and R.F. Tarrant, editors. The biology and management of red alder. Oregon State University Press, Corvallis, OR.

Bundt, M., M. Jaggi, P. Blaser, R. Siegwolf, and F. Hagedorn. 2001. Carbon and nitrogen dynamics in preferential flow paths and matrix of a forest soil. Soil Science Society of America Journal 65: 1529-1538.

Carreiro, M.M., R.L. Sinsabaugh, D.A. Repert, and D.F. Parkhurst. 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. Ecology 81: 2359-2365.

Chen, Q., C. Shen, S. Peng, Y. Sun, W. Ui, Z. Li, and M. Jiang. 2002. Soil organic matter turnover in the subtropical mountainous region of south China. Soil Science 167: 401-415.

Ehleringer, J.R., N. Buchmann, and L.B. Flanagan. 2000. Carbon isotope ratios in belowground carbon cycle processes. Ecological Applications 10: 412-422.

Emmett, B.A., O.J. Kjønaas, P. Gundersen, C. Koopmans, A. Tietema, and D. Sleep. 1998. Natural abundance of ^{15}N in forests across a nitrogen deposition gradient. Forest Ecology and Management 101: 9-18.

Evans, R.D. 2001. Physiological mechanisms influencing plant nitrogen isotope composition. Trends in Plant Science 6: 121-126.

Franklin, J.F., and C.T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press. Corvallis.

Garten, Jr., C.T. 1993. Variation in foliage ^{15}N abundance and the availability of soil nitrogen on Walker Branch Watershed. Ecology 74: 2098-2113.

Garten, Jr., C.T., and G.E. Taylor, Jr. 1992. Foliage $\delta^{13}C$ within a temperate deciduous forest: spatial, temporal, and species sources of variation. Oecologia 90: 1-7.

Garten, Jr., C.T., and H. Van Miegroet. 1994. Relationships between soil nitrogen dynamics and natural ^{15}N abundance in plant foliage from Great Smoky Mountains National Park. Canadian Journal of Forest Research 24: 1636-1645.

Hedin, L.O., J.C. von Fischer, N.E. Ostrom, B.P. Kennedy, M.G. Brown, and G.P. Robertson. 1998. Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil-stream interfaces. Ecology 79: 684-703.

Helfield, J.M., and R.J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology 82: 2403-2409.

Helfield, J.M., and R.J. Naiman. 2002. Salmon and alder as nitrogen sources to riparian forests in a boreal Alaskan watershed. Oecologia 133: 573-582.

Hobbie, E.A., and J. V. Colpaert. 2003. Nitrogen availability and colonization by mycorrhizal fungi correlate with nitrogen isotope patterns in plants. New Phytologist 157: 115-126.

Hobbie, E.A., S.A. Macko, and H.H. Shugart. 1999a. Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. Oecologia 118: 353-360.

Hobbie, E.A., S.A. Macko, and H.H. Shugart. 1999b. Interpretation of nitrogen isotope signatures using the NIFTE model. Oecologia 120: 405-415.

Hobbie, E.A., S.A. Macko, and M. Williams. 2000. Correlations between foliage $\delta^{15}N$ and nitrogen concentrations may indicate plant-mycorrhizal interactions. Oecologia 122: 273-283.

Hobbie, E.A., D.M. Olszyk, P.T. Rygiewicz, D.T. Tingey, and M.G. Johnson. 2001. Foliage nitrogen concentrations and natural abundance of ^{15}N suggest nitrogen allocation patterns of Douglas-fir and mycorrhizal fungi during development in elevated carbon dioxide concentration and temperature. Tree Physiology 21: 1113-1122.

Högberg, P. 1997. Tansley Review No. 95. ^{15}N natural abundance in soil-plant systems. New Phytologist 137: 179-203.

Hurd, T.M., D.J. Raynal, C.R. Schwintzer. 2001. Symbiotic N_2-fixation of *Alnus incana* ssp. *rugosa* in shrub wetlands of the Adirondack Mountains, New York, USA. Oecologia 126: 94-103.

Johannisson, C., and P. Högberg. 1994. ^{15}N abundance of soils and plants along an experimentally induced forest nitrogen supply gradient. Oecologia 97: 322-325.

Koba, K., M. Hirobe, L. Koyama, A. Kohzu, N. Tokuchi, K.J. Nadelhoffer, E. Wada, and H. Takeda. 2003. Natural ^{15}N abundance of plants and soil N in a temperate coniferous forest. Ecosystems 6:457-469.

Kohl, D.H., and G. Shearer. 1980. Isotopic fractionation associated with symbiotic N_2 fixation and uptake of NO_3^- by plants. Plant Physiology 66: 51-56.

Koopmans, C.J., D. van Dam, A. Tietema, and J.M. Verstraten. 1997. Natural ^{15}N abundance in two nitrogen saturated forest ecosystems. Oecologia 111: 470-480.

Luken, J.O., and R.W. Fonda. 1983. Nitrogen accumulation in a chronosequence of red alder communities along the Hoh River, Olympic National Park, Washington. Canadian Journal of Forest Research 13: 1228- 1237.

Marshall, J.D., and J. Zhang. 1994. Carbon isotope discrimination and water-use efficiency in native plants of the north-central Rockies. Ecology 75: 1887-1895.

McKane, R.B., L.C. Johnson, G.R. Shaver, K.J. Nadelhoffer, E.B. Rastetter, B. Fry, A.E. Giblin, K. Kielland, B.L. Kwiatkowski, J.A. Laundre, and G. Murray. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415: 68-71.

Michel, K. and E. Matzner. 2002. Nitrogen content of forest floor O_a layers affects carbon pathways and nitrogen mineralization. Soil Biology and Biochemistry 34: 1807-1813.

Nadelhoffer, K.J., and Fry, B. 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Science Society of America Journal 52: 1633-1640.

Nierenberg, T.R., and D.E. Hibbs, 1999. A characterization of unmanaged riparian areas in the central Coast Range of western Oregon. Forest Ecology and Management 129: 195-206.

Orr, E.L., W.N. Orr, and E.M. Baldwin. 1992. Geology of Oregon. Fourth edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Pabst, R.J., and T.A. Spies. 1999. Structure and composition of unmanaged riparian forests in the coastal mountains of Oregon, USA. Canadian Journal of Forest Research 29: 1557-1573.

Pardo, L.H., H.F. Hemond, J.P. Montoya, T.J. Fahey, and T.G. Siccama. 2002. Response of the natural abundance of ^{15}N in forest soils and foliage to high nitrate loss following clear-cutting. Canadian Journal of Forest Research 32: 1126-1136.

Peterson, B.J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecological Systems 18: 293-320.

Prescott, C.E. 2002. The influence of the forest canopy on nutrient cycling. Tree Physiology 22: 1193-1200.

Prescott, E.C., L.M. Zabek, C.L. Staley, and R. Kabzems. 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. Canadian Journal of Forest Research 30: 1742-1750.

Quideau, S.A., R.C. Graham, X. Feng, and O.A. Chadwick. 2003. Natural isotopic distribution in soil surface horizons differentiated by vegetation. Soil Science Society of America Journal 67: 1544-1550.

Reeves, G.H., K.M. Burnett, and S.V. Gregory. 2002. Fish and aquatic ecosystems of the Oregon Coast Range. Pages 68-98 *in* S.D. Hobbs, J.P. Hayes, R.L. Johnson, G.H. Reeves, T.A. Spies, J.C. Tappeiner, and G.E. Wells, editors. Forest and Stream Management in the Oregon Coast Range. Oregon State University Press, Corvallis, OR.

Reimchen, T.E., D.D. Mathewson, M.D. Hocking, J. Moran, and D. Harris. 2003. Isotopic evidence for enrichment of salmon-derived nutrients in vegetation, soil and insects in riparian zones in Coastal British Columbia. American Fisheries Society Symposium 34: 59-69.

Resh, S.C., D. Binkley, and J.A. Parrotta. 2002. Greater soil carbon sequestration under nitrogen-fixing trees compared with *Eucalyptus* species. Ecosystems 5: 217-231.

Robinson, D. 2001. $\delta^{15}N$ as an integrator of the nitrogen cycle. Trends Ecol. Evol. 16: 153- 162.

Rounick, J.S. and M.J. Winterbourn. 1986. Stable carbon isotopes and carbon flow in ecosystems. BioScience 36: 171-177.

Saiya-Cork, K.R., R.L. Sinsabaugh, and D.R. Zak. 2002. The effects of long term nitrogen deposition on extracellular enzyme activity in an *Acer saccharum* forest soil. Soil Biology and Biochemistry 34: 1309-1315.

SAS Institute Inc. (1999). SAS OnlineDoc, Version 8 Edition. Cary, NC.

Shearer, G., and D.H. Kohl. 1986. N_2-fixation in field settings: estimations based on natural ^{15}N abundance. Australian Journal of Plant Physiology 13: 699-756.

Spies, T.A., D.E. Hibbs, J.L. Ohmann, G.H. Reeves, R.J. Pabst, F.J. Swanson, C. Whitlock, J.A. Jones, B.C. Wemple, L.A. Parendes, and B.A. Schrader. 2002. The ecological basis of forest ecosystem management in the Oregon Coast Range. Pages 31-67 *in* S.D. Hobbs, J.P. Hayes, R.L. Johnson, G.H. Reeves, T.A. Spies, J.C. Tappeiner, and G.E. Wells, editors. Forest and Stream Management in the Oregon Coast Range. Oregon State University Press, Corvallis, OR.

Turner, B., D.W. Cole, and S.P. Gessel. 1976. Mineral nutrient accumulation and cycling in a stand of red alder (*Alnus rubra*). Journal of Ecology, 64: 965-974.

Van Miegroet, H., and D.W. Cole. 1984. Acidification sources in red alder and Douglas-fir soils – importance of nitrification. Soil Science Society of America Journal 49: 1274-1279.

Vitousek, P.M., K. Cassman, C. Cleveland, T. Crews, C.B. Field, N.B. Grimm, R.W. Howarth, R.Marino, L Martinelli, E.B. Rastetter, and J.I. Sprent. 2002. Towards an ecological understanding of biological nitrogen fixation. Biogeochemistry 57/58: 1-45.

Vitousek, P.M., and R.W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13: 87-115.

Vogel, J.G., and S.T. Gower. 1998. Carbon and nitrogen dynamics of boreal jack pine stands with and without a green alder understory. Ecosystems 1: 386-400.

Volk, C.J., P.M. Kiffney, and R.L. Edmonds. 2003. Role of riparian red alder in the nutrient dynamics of coastal streams of the Olympic Peninsula, Washington, USA. American Fisheries Society Symposium 34: 213-225.

Wedin, D.A., L.L. Tieszen, B. Dewey, and J. Pastor. 1995. Carbon isotope dynamics during grass decomposition and soil organic matter formation. Ecology 76: 1383-1392.

CONCLUSION

The objectives of this thesis were to determine the utility of natural abundance stable isotopes of nitrogen and carbon in food web analyses and describe nutrient dynamics and source-sink relationships in red alder- and Douglas-fir-dominated riparian areas of the central Oregon Coast Range. To do this, we addressed the variation in stable isotopes of N and C in Douglas-fir and red alder foliage across three spatial scales (i.e. within a crown, within a site, and among sites), analyzed the isotope signature of foliage through different stages (i.e. foliage, litterfall, and forest floor material), and compared foliage $\delta^{15}N$ and $\delta^{13}C$ with that of soils in riparian forests. The results of this research suggested $\delta^{15}N$ and $\delta^{13}C$ had limited use in food web analyses with red alder and Douglas-fir at our riparian sites but did provide useful information about nitrogen dynamics and source-sink relationships between soils and Douglas-fir or red alder.

The level of variation in $\delta^{15}N$ and $\delta^{13}C$ and the similarity of isotope values between Douglas-fir and red alder at our sites would make it difficult to distinguish between food webs based on these species. As an exploratory analysis, we analyzed the isotope composition of several invertebrate species that were captured at three of our sites: two red alder-dominated sites and one dominated by Douglas-fir (Figure 4.1; invertebrates provided by Holly Ober, another ARMACS graduate student). The invertebrates consisted of several species of moths (*Lophocampa maculata, Nadata gibbosa, Antheraea polyphemus*), adult caddisflies (*Limnephilidae*), and larval caddisflies (*Psychoglypha*). The data are limited in their usefulness because the dietary sources of the invertebrates analyzed are unknown and may entail a combination of plant species, both terrestrial and aquatic. Also, the small sample size of understory species on each site does not provide information on the range of $\delta^{15}N$ and $\delta^{13}C$ that invertebrates may be consuming when feeding on these species. Nevertheless, the data demonstrate the difficulty of

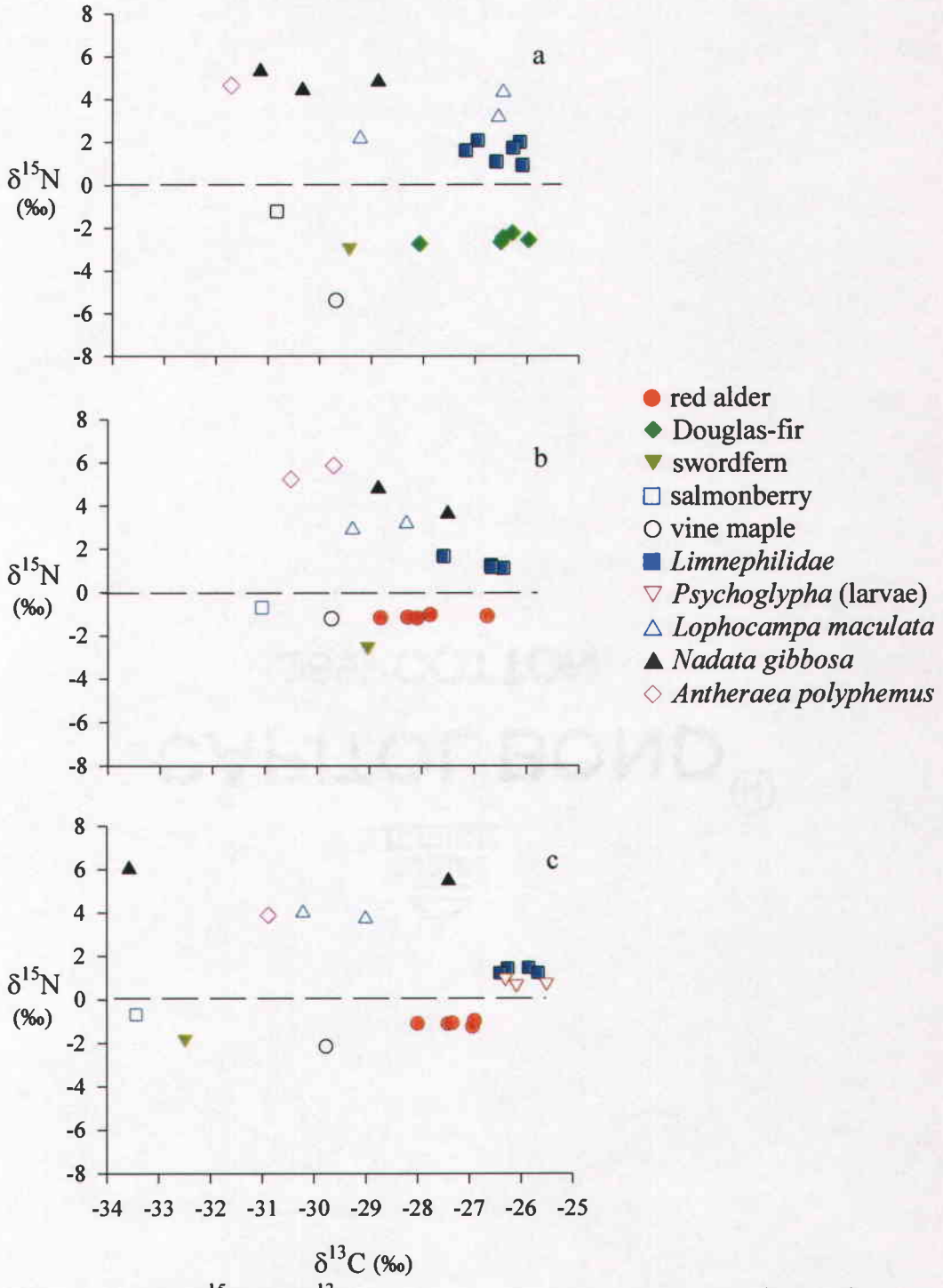

Figure 4.1. The $\delta^{15}N$ and $\delta^{13}C$ of invertebrates, understory vegetation, and Douglas-fir or red alder at Wolf (a), Nelson (b), and Honey Grove (c) Creeks. Each point represents one sample.

determining between red alder or Douglas-fir as food sources at our sites. Food web research on the western side of the Olympic Peninsula, WA, has been more successful using $\delta^{15}N$ and $\delta^{13}C$ to distinguish between red alder and conifer food webs (Carol Volk, unpublished data). Their conifer (western hemlock and western redcedar) and red alder $\delta^{15}N$ were less similar than the $\delta^{15}N$ found at our sites (conifers < –3.4‰, red alder = -2.4‰ and -1.6‰) allowing for greater distinction between the vegetation.

The broad use of stable isotopes to identify food webs based on either Douglas-fir or red alder would not substitute for more traditional food web analyses at our sites. However, stable isotopes may still be useful for other food web questions incorporating sources in addition to Douglas-fir or red alder. For example, there was less overlap in $\delta^{13}C$ between the understory and canopy species than between red alder and Douglas-fir. This suggests $\delta^{13}C$ could distinguish organisms feeding on understory versus canopy vegetation. Also, aquatic food sources, such as algae, may be isotopically distinct from red alder and Douglas-fir at our sites and could provide information on the amount of autochthonous versus allochthonous material consumed by aquatic organisms. Finally, stable isotopes could help determine the proportions of an omnivore's diet that came from plant versus animal sources.

Stable isotope analysis demonstrated red alder's ability to amend soil $\delta^{15}N$ with high inputs of N-rich litter derived from N_2-fixation. On our Douglas-fir sites, the soil $\delta^{15}N$ and N availability gradients with distance from the stream suggested red alder had previously occurred along the stream and influenced soil N availability and $\delta^{15}N$. Analyzing past aerial photos of the Douglas-fir sites would further identify whether red alder had previously occurred along these streams to influence the soil N gradients.

The influence of marine N from spawning salmonids was not detected with $\delta^{15}N$ at our sites. Our data do not rule out the possibility of marine N inputs at our sites; however, high N inputs from red alder may decrease the relative importance

of marine N for vegetation on our sites compared to other sites where red alder is less prevalent. Salmon carcasses may contribute other limiting nutrients, such as phosphorus, to these riparian areas that our study did not address.

The scope of inference of this research is limited to the ten sites we studied in the Oregon Coast Range and the trees we sampled at the Siletz plantation. Further research at a greater number of sites would help determine if the patterns of isotope variation in foliage, litter, and soil as well as the gradient of N availability at the riparian Douglas-fir sites were applicable to more of the Oregon Coast Range. Although we purposefully selected sites dominated by either red alder or Douglas-fir in an attempt to maximize isotope differences between the species, a large portion of riparian areas in the Oregon Coast Range are mixtures of both species. It is unclear whether the patterns we found would be the same under a mixed-species overstory.

The influence of red alder on the gradients of N-availability and soil $\delta^{15}N$ at Douglas-fir sites demonstrated its importance to these riparian systems in N-dynamics. Although red alder may not supply large wood to streams like Douglas-fir, removing or significantly reducing red alder in riparian areas would remove a large source of N to this ecosystem and should be considered by managers regarding hardwood conversions.

BIBLIOGRAPHY

Adams, M.A., and P.F. Grierson. 2001. Stable isotopes at natural abundance in terrestrial plant ecology and ecophysiology: an update. Plant biology 3: 299-310.

Allan, J.D., M.S. Wipfli, J.P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences 60: 309-320.

Balesdent, J., C. Girardin, and A. Mariotti. 1993. Site-related $\delta^{13}C$ of tree leaves and soil organic matter in a temperate forest. Ecology 74: 1713-1721.

Beaupied, H., A. Moiroud, A. Domenach, F. Kurdali, and R. Lensi. 1990. Ratio of fixed and assimilated nitrogen in a black alder (*Alnus glutinosa*) stand. Canadian Journal of Forest Research 20: 1116-1119.

Ben-David, M., R.W. Flynn, and D.M. Schell. 1997. Annual and seasonal changes in diets of martens; evidence from stable isotope analysis. Oecologia 111: 280-291.

Ben-David, M., T.A. Hanley, and D.M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. Oikos 83: 47-55.

Bilby, R.E., E.W. Beach, B.R. Fransen, J.K. Walter, and P.A. Bisson. 2003. Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. Transactions of American Fisheries Society 132: 733-745.

Bilby, R.E., B.R. Fransen, and P.A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53: 164-173.

Binkley, D., K. Cromack, Jr., and D.D. Baker. 1994. Nitrogen fixation by red alder: biology, rates, and controls. Pages 57-72 *in* D.E. Hibbs, D.S. DeBell, and R.F. Tarrant, editors. The biology and management of red alder. Oregon State University Press, Corvallis, OR.

Binkley, D., P. Sollins, R. Bell, D. Sachs, and D. Myrold. 1992. Biogeochemistry of adjacent conifer and alder-conifer stands. Ecology 73: 2022-2033.

Binkley, D., P. Sollins, and W.B. McGill. 1985. Natural abundance of nitrogen-15 as a tool for tracting alder-fixed nitrogen. Soil Science Society of America Journal. 49: 444-447.

Bormann, B.T., K. Cormack, Jr., and W.O. Russell III.1994. Influences of red alder on soils and long-term ecosystem productivity. Pages 47-56 *in* D.E. Hibbs, D.S. DeBell, and R.F. Tarrant, editors. The biology and management of red alder. Oregon State University Press, Corvallis, OR.

Brooks, J.R., D.G. Sprugel, and T.M. Hinckley. 1996. The effects of light acclimation during and after foliage expansion on photosynthesis and *Abies amabilis* foliage within the canopy. Oecologia 107: 21-32.

Buchmann, N., W. Kao, and J. Ehleringer. 1997. Influence of stand structure on carbon-13 of vegetation, soils, and canopy air within deciduous and evergreen forests in Utah, United States. Oecologia 110: 109-119.

Bundt, M., M. Jaggi, P. Blaser, R. Siegwolf, and F. Hagedorn. 2001. Carbon and nitrogen dynamics in preferential flow paths and matrix of a forest soil. Soil Science Society of America Journal 65: 1529-1538.

Carreiro, M.M., R.L. Sinsabaugh, D.A. Repert, and D.F. Parkhurst. 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. Ecology 81: 2359-2365.

Cerling, T.E., J.M Harris, M.G. Leakey. 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. Oecologia 120: 364-374.

Chan, S.S., S.R. Radosevich, and A.T. Grotta. 2003. Effects of contrasting light and soil moisture availability on the growth and biomass allocation of Douglas-fir and red alder. Canadian Journal of Forest Research 33: 106-117.

Chen, Q., C. Shen, S. Peng, Y. Sun, W. Ui, Z. Li, and M. Jiang. 2002. Soil organic matter turnover in the subtropical mountainous region of south China. Soil Science 167: 401-415.

Cherel, Y., K.A. Hobson, and H. Weimerskirch. 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122: 155-162.

Dawson, T.E., S. Mambelli, A.H. Planboeck, P.H. Templer, and K.P. Tu. 2002. Stable isotopes in plant ecology. Annual Review of Ecology and Systematics 33: 507-559.

DeNiro, M.J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42: 495-506.

DeNiro, M.J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45: 341-351.

Domenach, A.M., F.Kurdali, and R. Bardin. 1989. Estimationof symbiotic dinitrigen fixation in alder forest by the method based on natural ^{15}N abundance. Plant and Soil 118: 51-59.

Ehleringer, J.R., N. Buchmann, and L.B. Flanagan. 2000. Carbon isotope ratios in belowground carbon cycle processes. Ecological Applications 10: 412-422.

Emmett, B.A., O.J. Kjønaas, P. Gundersen, C. Koopmans, A. Tietema, and D. Sleep. 1998. Natural abundance of ^{15}N in forests across a nitrogen deposition gradient. Forest Ecology and Management 101: 9-18.

Evans, R.D. 2001. Physiological mechanisms influencing plant nitrogen isotope composition. Trends in Plant Science 6: 121-126.

Farquhar, G.D., M.H. O'Leary, and J.A. Berry. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology 9: 121-137.

Fessenden, J.E., and J.E. Ehleringer. 2002. Age-related variations in $\delta^{13}C$ of ecosystem respiration across a coniferous forest chronosequence in the Pacific Northwest. Tree Physiology 22: 159-167.

Fessenden, J.E., and J.E. Ehleringer. 2003. Temporal variation in $\delta^{13}C$ of ecosystem respiration in the Pacific Northwest: links to moisture stress. Oecologia 136: 129-136.

Franklin, J.F., and C.T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press. Corvallis.

Garten, Jr., C.T. 1993. Variation in foliage ^{15}N abundance and the availability of soil nitrogen on Walker Branch Watershed. Ecology 74: 2098-2113.

Garten, Jr., C.T., and G.E. Taylor, Jr. 1992. Foliage $\delta^{13}C$ within a temperate deciduous forest: spatial, temporal, and species sources of variation. Oecologia 90: 1-7.

Garten, Jr., C.T., and H. Van Miegroet. 1994. Relationships between soil nitrogen dynamics and natural ^{15}N abundance in plant foliage from Great Smoky Mountains National Park. Canadian Journal of Forest Research 24: 1636-1645.

Gebauer, G., and E.D. Schulze. 1991. Carbon and nitrogen isotope ratios in different compartments of a healthy and a declining *Picea abies* forest in the Fichtelgebirge, NE Bavaria. Oecologia 87: 198-207.

Gregory, S.V., F. J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. Focus on links between land and water. Bioscience 8: 540-551.

Grogan, P., T.D. Bruns, and F.S. Chapin III. 2000. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. Oecologia 122: 537-544.

Hedin, L.O., J.C. von Fischer, N.E. Ostrom, B.P. Kennedy, M.G. Brown, and G.P. Robertson. 1998. Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil-stream interfaces. Ecology 79: 684-703.

Helfield, J.M., and R.J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology 82: 2403-2409.

Helfield, J.M., and R.J. Naiman. 2002. Salmon and alder as nitrogen sources to riparian forests in a boreal Alaskan watershed. Oecologia 133: 573-582.

Herrera M., L.G., K.A. Hobson, L. Miron M., N. Ramirez P., G. Mendez C., and V. Sanchez-Cordero. 2001. Sources of protein in two species of phytophagous bats in a seasonal dry forest: evidence from stable-isotope analysis. Journal of Mammalogy 82: 352-361.

Hobbie, E.A., and J. V. Colpaert. 2003. Nitrogen availability and colonization by mycorrhizal fungi correlate with nitrogen isotope patterns in plants. New Phytologist 157: 115-126.

Hobbie, E.A., S.A. Macko, and H.H. Shugart. 1999a. Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. Oecologia 118: 353-360.

Hobbie, E.A., S.A. Macko, and H.H. Shugart. 1999b. Interpretation of nitrogen isotope signatures using the NIFTE model. Oecologia 120: 405-415.

Hobbie, E.A., S.A. Macko, and M. Williams. 2000. Correlations between foliage $\delta^{15}N$ and nitrogen concentrations may indicate plant-mycorrhizal interactions. Oecologia 122: 273-283.

Hobbie, E.A., D.M. Olszyk, P.T. Rygiewicz, D.T. Tingey, and M.G. Johnson. 2001. Foliage nitrogen concentrations and natural abundance of ^{15}N suggest nitrogen allocation patterns of Douglas-fir and mycorrhizal fungi during development in elevated carbon dioxide concentration and temperature. Tree Physiology 21: 1113-1122.

Hobson, K.A. 1995. Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. The Condor 97: 752-762.

Högberg, P. 1997. Tansley Review No. 95. ^{15}N natural abundance in soil-plant systems. New Phytol. 137: 179-203.

Hurd, T.M., D.J. Raynal, C.R. Schwintzer. 2001. Symbiotic N_2-fixation of *Alnus incana* ssp. *rugosa* in shrub wetlands of the Adirondack Mountains, New York, USA. Oecologia 126: 94-103.

Hutchings, M.J., E.A. John, and A.J.A. Stewart (editors). 1999. The Ecological Consequences of Environmental Heterogeneity. The 40th Symposium of the British Ecological Society, University of Sussex.

Johannisson, C., and P. Högberg. 1994. ^{15}N abundance of soils and plants along an experimentally induced forest nitrogen supply gradient. Oecologia 97: 322-325.

Koba, K., M. Hirobe, L. Koyama, A. Kohzu, N. Tokuchi, K.J. Nadelhoffer, E. Wada, and H. Takeda. 2003. Natural ^{15}N abundance of plants and soil N in a temperate coniferous forest. Ecosystems 6:457-469.

Koerner, W., E. Dambrine, J.L. Dupouey, and M. Benoît. 1999. $\delta^{15}N$ of forest soil and understorey vegetation reflect the former agricultural land use. Oecologia 121: 421-425.

Kohl, D.H., and G. Shearer. 1980. Isotopic fractionation associated with symbiotic N_2 fixation and uptake of NO_3^- by plants. Plant Physiology 66: 51-56.

Koopmans, C.J., D. van Dam, A. Tietema, and J.M. Verstraten. 1997. Natural ^{15}N abundance in two nitrogen saturated forest ecosystems. Oecologia 111: 470-480.

Luken, J.O., and R.W. Fonda. 1983. Nitrogen accumulation in a chronosequence of red alder communities along the Hoh River, Olympic National Park, Washington. Canadian Journal of Forest Research 13: 1228- 1237.

Le Roux, X., T. Bariac, H. Sinoquet, B. Genty, C. Piel, A. Mariotti, C. Girardin, and P. Richard. 2001. Spatial distribution of leaf water-use efficiency and carabon isotope discrimination within an isolated tree crown. Plant, Cell, and Environment 24: 1021-1032.

Marshall, J.D., and J. Zhang. 1994. Carbon isotope discrimination and water-use efficiency in native plants of the north-central Rockies. Ecology 75: 1887-1895.

McComb, W.C. 1994. Red alder: interactions with wildlife. *In* The biology and management of red alder. Pages 131-138 *in* D.E. Hibbs, D.S. DeBell, and R.F. Tarrant, editors. The biology and management of red alder. Oregon State University Press, Corvallis, OR.

McIlwee, A.P., and C.N. Johnson. 1998. The contribution of fungus to the diets of three mycophagous marsupials in *Eucalyptus* forests, revealed by stable isotope analysis. Functional Ecology 12: 223-231.

McKane, R.B., L.C. Johnson, G.R. Shaver, K.J. Nadelhoffer, E.B. Rastetter, B. Fry, A.E. Giblin, K. Kielland, B.L. Kwiatkowski, J.A. Laundre, and G. Murray. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415: 68-71.

Michel, K. and E. Matzner. 2002. Nitrogen content of forest floor Oa layers affects carbon pathways and nitrogen mineralization. Soil Biology and Biochemistry 34: 1807-1813.

Nadelhoffer, K.J., and Fry, B. 1988. Controls on natural nitrogen-15 and Carbon-13 abundances in forest soil organic matter. Soil Science Society of America Journal 52: 1633-1640.

Nierenberg, T.R., and D.E. Hibbs, 1999. A characterization of unmanaged riparian areas in the central Coast Range of western Oregon. Forest Ecology and Management 129: 195-206.

Orr, E.L., W.N. Orr, and E.M. Baldwin. 1992. Geology of Oregon. Fourth edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Pabst, R.J., and T.A. Spies. 1999. Structure and composition of unmanaged riparian forests in the coastal mountains of Oregon, USA. Canadian Journal of Forest Research 29: 1557-1573.

Panek, Jeanne A. and R.H. Waring. 1995. Carbon isotope variation in Douglas-fir foliage: improving the $\delta^{13}C$-climate relationship. Tree Physiology 15: 657-663.

Panek, Jeanne A. and R.H. Waring. 1997. Stable carbon isotopes as indicators of limitations to forest growth imposed by climate stress. Ecological Applications. 7: 854-863.

Pardo, L.H., H.F. Hemond, J.P. Montoya, T.J. Fahey, and T.G. Siccama. 2002. Response of the natural abundance of ^{15}N in forest soils and foliage to high nitrate loss following clear-cutting. Canadian Journal of Forest Research 32: 1126-1136.

Peterson, B.J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecological Systems 18: 293-320.

Phillips, D.L. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. Oecologia 127: 166-170.

Phillips, D.L., and J.W. Gregg. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127: 171-179.

Phillips, D.L., and P.L. Koch. 2002. Incorporating concentration dependence in stable isotope mixing models. Oecologia 130: 114-125.

Piccolo, J.J., and M.S. Wipfli. 2002. Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export from headwater streams to downstream habitats in southeastern Alaska? Canadian Journal of Fisheries and Aquatic Sciences 59: 503-513.

Polischuk, S.C., K.A. Hobson, and M.A. Ramsay. 2001. Use of stable-carbon and –nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. Canadian Journal of Zoology 79: 499-511.

Ponsard, S., and R. Arditi. 2000. What can stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) tell about the food web of soil macro-invertebrates? Ecology 81: 852-864.

Ponton, S., J.-L. Dupouey, N. Breda, F. Feuillat, C. Bodenes, and E. Dreyer. 2001. Carbon isotope discrimination and wood anatomy variations in mixed stands of *Quercus robur* and *Quercus petraea*. Plant, Cell and Environment 24: 861-868.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703-718.

Prescott, C.E. 2002. The influence of the forest canopy on nutrient cycling. Tree Physiology 22: 1193-1200.

Prescott, E.C., L.M. Zabek, C.L. Staley, and R. Kabzems. 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. Canadian Journal of Forest Research 30: 1742-1750.

Quideau, S.A., R.C. Graham, X. Feng, and O.A. Chadwick. 2003. Natural isotopic distribution in soil surface horizons differentiated by vegetation. Soil Science Society of America Journal 67: 1544-1550.

Reeves, G.H., K.M. Burnett, and S.V. Gregory. 2002. Fish and aquatic ecosystems of the Oregon Coast Range. Pages 68-98 *in* S.D. Hobbs, J.P. Hayes, R.L. Johnson, G.H. Reeves, T.A. Spies, J.C. Tappeiner, and G.E. Wells, editors. Forest and Stream Management in the Oregon Coast Range. Oregon State University Press, Corvallis, OR.

Reimchen, T.E., D.D. Mathewson, M.D. Hocking, J. Moran, and D. Harris. 2003. Isotopic evidence for enrichment of salmon-derived nutrients in vegetation, soil and insects in riparian zones in Coastal British Columbia. American Fisheries Society Symposium 34: 59-69.

Resh, S.C., D. Binkley, and J.A. Parrotta. 2002. Greater soil carbon sequestration under nitrogen-fixing trees compared with *Eucalyptus* species. Ecosystems 5: 217-231.

Richardson, J.S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology 72: 873-887.

Robinson, D. 2001. $\delta^{15}N$ as an integrator of the nitrogen cycle. Trends in Ecology and Evolution 16: 153- 162.

Rounick, J.S. and M.J. Winterbourn. 1986. Stable carbon isotopes and carbon flow in ecosystems. BioScience 36: 171-177.

Saiya-Cork, K.R., R.L. Sinsabaugh, and D.R. Zak. 2002. The effects of long term nitrogen deposition on extracellular exzyme activity in an *Acer saccharum* forest soil. Soil Biology and Biochemistry 34: 1309-1315.

SAS Institute Inc. (1999). SAS OnlineDoc, Version 8 Edition. Cary, NC.

Shearer, G., and D.H. Kohl. 1986. N_2-fixation in field settings: estimations based on natural ^{15}N abundance. Australian Journal of Plant. Physiology 13: 699-756.

Spies, T.A., D.E. Hibbs, J.L. Ohmann, G.H. Reeves, R.J. Pabst, F.J. Swanson, C. Whitlock, J.A. Jones, B.C. Wemple, L.A. Parendes, and B.A. Schrader. 2002. The ecological basis of forest ecosystem management in the Oregon Coast Range. Pages 31-67 *in* S.D. Hobbs, J.P. Hayes, R.L. Johnson, G.H. Reeves, T.A. Spies, J.C. Tappeiner, and G.E. Wells, editors. Forest and Stream Management in the Oregon Coast Range. Oregon State University Press, Corvallis, OR.

Sternberg, L., S.S. Mulkey, and S.J. Wright. 1989. Ecological interpretation of leaf carbon isotope ratios: influence of respired carbon dioxide. Ecology 70: 1317-1324.

Stewart, G.R., M.H. Turnbull, S. Schmidt, and P.D. Erskine. 1995. ^{13}C natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. Australian Journal of Plant Physiology 22: 51-55.

Sutherland, R.A., C. van Kessel, R.E. Farrell, and D.J. Pennock. 1993. Landscape-scale variations in plant and soil nitrogen-15 natural abundance. Soil Science Society of America Journal 57: 169-178.

Sydeman, W.J., K.A. Hobson, P. Pyle, and E.B. McLaren. 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. The Condor 99: 327-336.

Tieszen, L.L., T.W. Boutton, K.G. Tesdahl, and N.A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia 57: 32-37.

Turner, B., D.W. Cole, and S.P. Gessel. 1976. Mineral nutrient accumulation and cycling in a stand of red alder (*Alnus rubra*). Journal of Ecology, 64: 965-974.

Van Miegroet, H., and D.W. Cole. 1984. Acidification sources in red alder and Douglas-fir soils – importance of nitrification. Soil Science Society of America Journal 49: 1274-1279.

Vander Zanden, M.J., and J.B. Rasmussen. 1999. Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology 80: 1395-1404.

Vitousek, P.M., K. Cassman, C. Cleveland, T. Crews, C.B. Field, N.B. Grimm, R.W. Howarth, R.Marino, L Martinelli, E.B. Rastetter, and J.I. Sprent. 2002. Towards an ecological understanding of biological nitrogen fixation. Biogeochemistry 57/58: 1-45.

Vogel, J.G., and S.T. Gower. 1998. Carbon and nitrogen dynamics of boreal jack pine stands with and without a green alder understory. Ecosystems 1: 386-400.

Volk, C.J., P.M. Kiffney, and R.L. Edmonds. 2003. Role of riparian red alder in the nutrient dynamics of coastal streams of the Olympic Peninsula, Washington, USA. American Fisheries Society Symposium 34: 213-225.

Warren, C.R., and M.A. Adams. 2001. Distribution of N, Rubisco and photosynthesis in *Pinus pinaster* and acclimation to light. Plant, Cell and Environment 24: 597-609.

Warren, C.R., G.J. Ethier, N.J. Livingston, N.J. Grant, D.H. Turpin, D.L. Harrison, and T.A. Black. 2003. Transfer conductance in second growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.)Franco) canopies. Plant, Cell and Environment 26: 1215-1227.

Waring, R.H. and W.B. Silvester. 1994. Variation in foliage $\delta^{13}C$ values within the crowns of *Pinus radiata* trees. Tree Physiology 14: 1203-1213.

Wedin, D.A., L.L. Tieszen, B. Dewey, and J. Pastor. 1995. Carbon isotope dynamics during grass decomposition and soil organic matter formation. Ecology 76: 1383-1392.

Wigington, Jr., P.J., M.R. Church, T.C. Strickland, K.N. Eshleman, and J. Van Sickle. 1998. Autumn chemistry of Oregon Coast Range streams. Journal of American Water Resources Association 34: 1035-1049.

Wipfli, M.S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences. 54: 1259-1269.

Wolf, B., Martinez del Rio, C. 2000. Use of saguaro fruit by white-winged doves: isotopic evidence of a tight ecological association. Oecologia 124: 536-543.

APPENDIX

Relationship between $\delta^{15}N$ and %N

Figures A1.1 and A1.2 describe the relationship between $\delta^{15}N$ and %N of 10 plantation Douglas-fir and red alder trees, respectively. The $\delta^{15}N$ of foliage may vary in response to foliage %N if proteins comprise a greater proportion of the N content. Proteins are more enriched in ^{15}N relative to other organic compounds such as chlorophyll, cell wall compounds, lipids, and alkaloids (Werner and Schmidt 2002).

Relationship between $\delta^{13}C$ and %N

Figures A1.3 and A1.4 describe the relationship between $\delta^{13}C$ and %N of 10 plantation Douglas-fir and red alder trees, respectively. Plants in high N environments may have better water use efficiency than plants of the same species in low N environments due to high rates of carbon fixation relative to water loss.

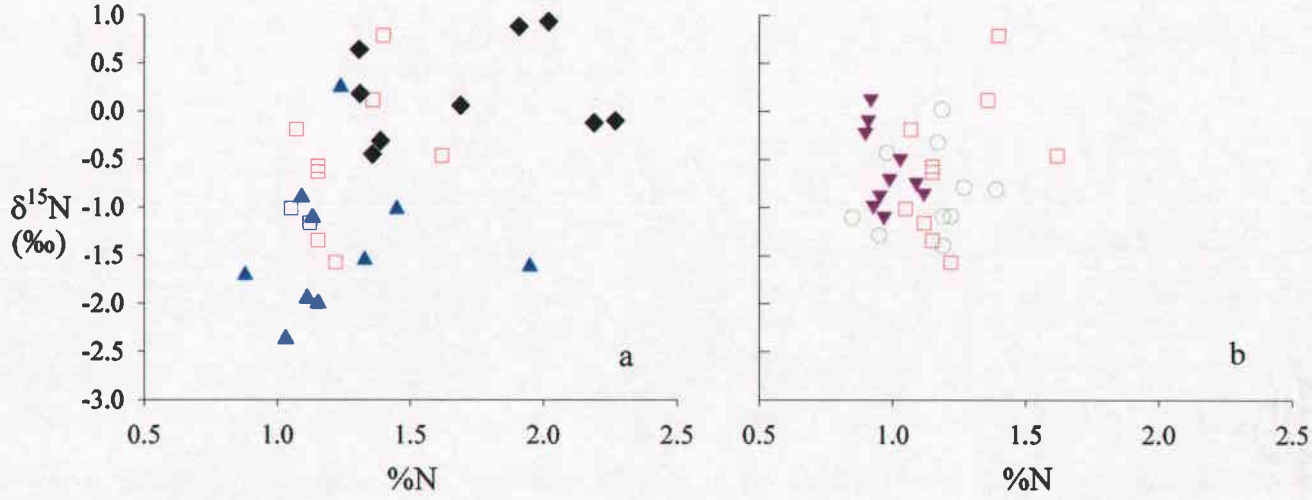

Figure A1.1. The $\delta^{15}N$ and %N of Douglas-fir needles from 10 plantation trees. Symbols are: a) 1 year top (◆), 1 year middle (□), 1 year bottom (▲); b) 1 year middle (□), 2 year middle (○), 3 year middle (▼).

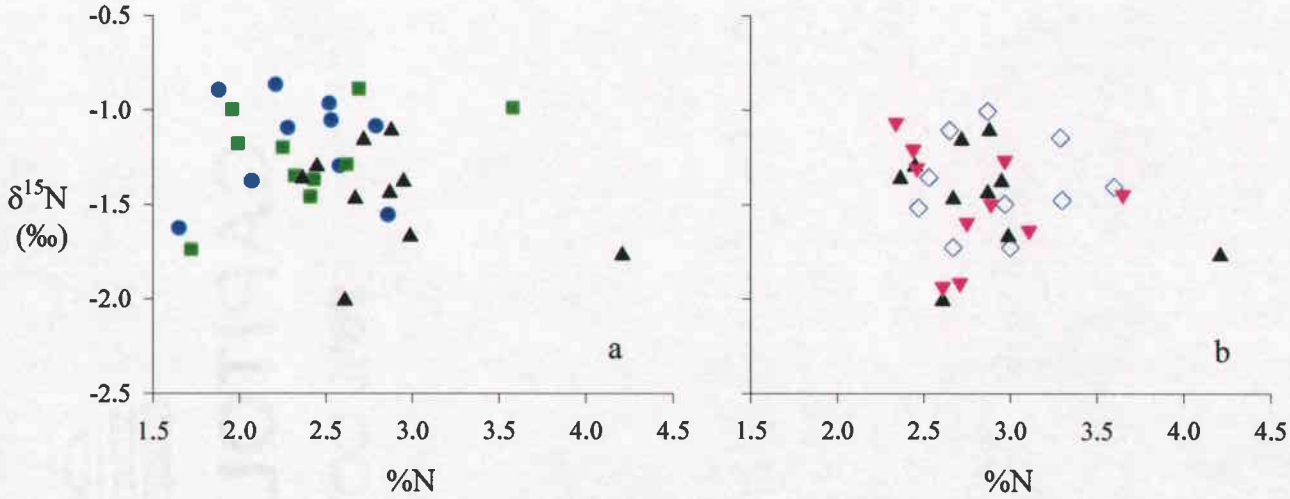

Figure A1.2. The $\delta^{15}N$ and %N of red alder leaves from 10 plantation trees. Symbols are: a) edge top (●), edge middle (■), edge bottom (▲); b) edge bottom (▲), center bottom (◇), trunk bottom (▼).

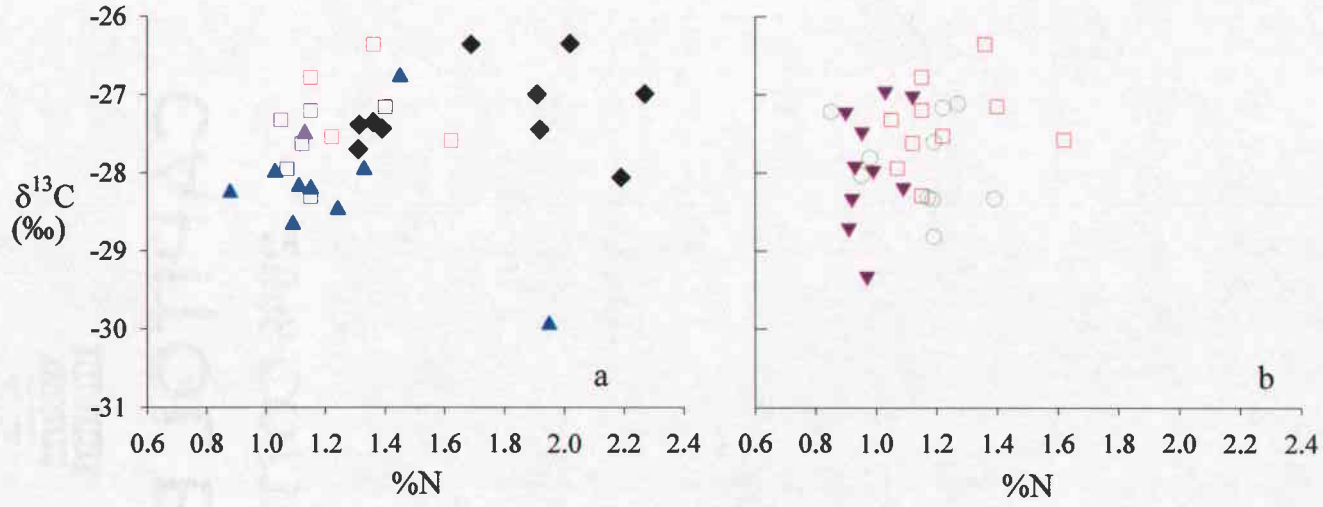

Figure A1.3. The $\delta^{13}C$ and %N of Douglas-fir needles from 10 plantation trees. Symbols are: a) 1 year top (◆), 1 year middle (□), 1 year bottom (▲); b) 1 year middle (□), 2 year middle (○), 3 year middle (▼).

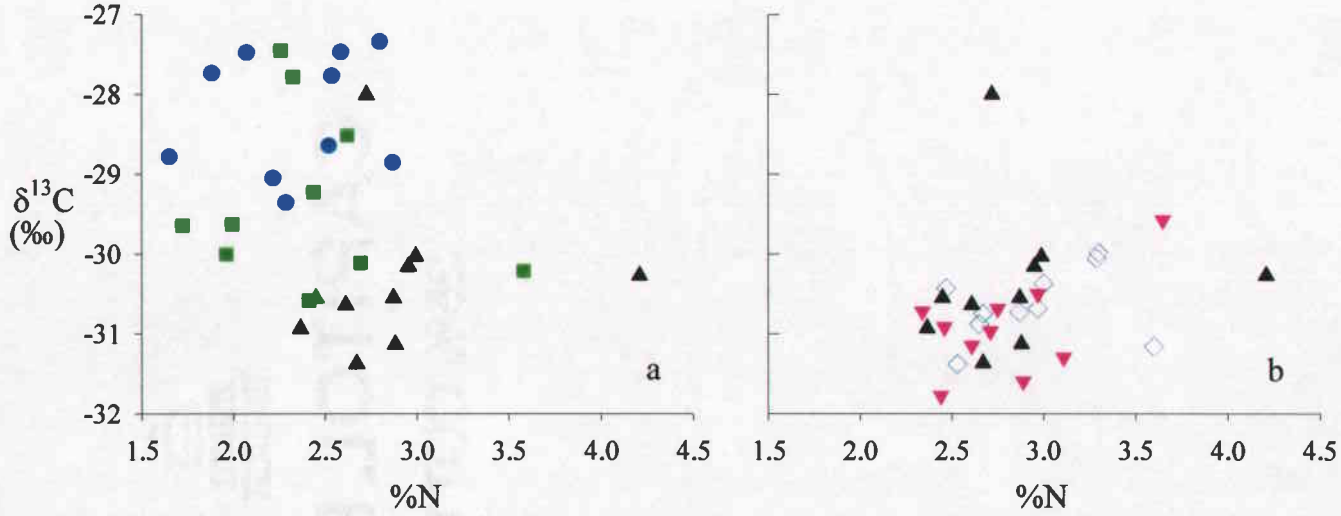

Figure A1.4. The $\delta^{13}C$ and %N of red alder leaves from 10 plantation trees. Symbols are: a) edge top (●), edge middle (■), edge bottom (▲); b) edge bottom (▲), center bottom (◇), trunk bottom (▼).

Table A.1. Soil characteristics of riparian sites.

Site	Soil series of stream and surrounding area	Classification
Alsea tributary*		
	Bohannon (Btf)	Fine-Loamy, Mixed, Mesic Andic Haplumbrepts
	Blachly (Bce)	Fine, Mixed, Mesic Umbric Dystrochrepts
	Preacher (Phe)	Fine-Loamy, Mixed, Mesic Andic Haplumbrepts
Yew Creek*		
	Colluvial (Cu)	Inceptisols
	Klickatat (Kmf)	Loamy-Skeletal, Mixed, Mesic Typic Haplumbretps
	Klickatat (Kmg)	Loamy-Skeletal, Mixed, Mesic Typic Haplumbretps
Trout Creek*		
	Colluvial (Cu)	Inceptisols
	Hatchery (Haf)	Loamy-Skeletal, Mixed, Mesic Dystric Eutrochrepts
	Hatchery-Honey Grove complex (HgE)	Loamy-Skeletal, Mixed, Mesic Dystric Eutrochrepts
South Fork of Alsea*		
	Colluvial (Cu)	Inceptisols
	Hatchery (Haf)	Loamy-Skeletal, Mixed, Mesic Dystric Eutrochrepts
	Honey Grove clay (HtD)	Clayey, Mixed, Mesic Typic Palehumults
Honey Grove*		
	Colluvial (Cu)	Inceptisols
	Digger (DIG)	Loamy-Skeletal, Mixed, Mesic Dystric Eutrochrepts
	Apt clay (AdF)	Clayey, Mixed, Mesic Typic Haplohumults
Coleman Creek*		
	Colluvial (Cu)	Inceptisols
	Landslide slickrock (LS)	Medial Over Loamy, Mixed, Mesic Alic Fulvudands
	Bohannon (BMF)	Fine-loamy, Mixed, Mesic Andic Haplumbrepts
Record Creek*		
	Colluvial (Cu)	Inceptisols
	Apt clay (AcE)	Clayey, Mixed, Mesic Typic Haplohumults
	Digger (DIF)	Loamy-Skeletal, Mixed, Mesic Dystric Eutrochrepts
Nelson Creek†		
	Meda (82C)	Fine-Loamy, Mixed, Mesic Typic Haplumbrepts
	Preacher (111F)	Fine-Loamy, Mixed, Mesic Andic Haplumbrepts
	Bohannon (16H)	Fine-Loamy, Mixed, Mesic Typic Haplumbrepts
Wolf Creek†		
	Eilertsen (46)	Fine-Silty, Mixed, Mesic Ultic Hapludalfs
	Bohannon (16H)	Fine-Loamy, Mixed, Mesic Typic Haplumbrepts
Smith Creek†		
	Dupee (45C)	Fine, Mixed, Mesic Aquultic Haploxeralfs
	Digger (40H)	Loamy-Skeletal, Mixed, Mesic Dystric Eutrochrepts
	Bellpine (11E)	Clayey, Mixed, Mesic Xeric Haplohumults

*Corliss, J.F. 1973. *Soil Survey of Alsea Area, Oregon.* (Washington, D.C.: USDA Soil Conservation Service).

†Patching, W.R. 1987. *Soil Survey of Lane County Area, Oregon.* (Washington, D.C.: USDA Soil Conservation Service).