Litter Decay in Coast Range Riparian Zones: Biogeochemical Controls and Implications for Terrestrial and Aquatic Food Chains

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Decomposition of leaf litter plays a vital role in riparian zone function. Both aquatic and terrestrial food chains rely on energy and nutrients derived from riparian forests. In order to increase long-term supplies of structural large wood to streams, many forest managers in western Oregon encourage the conversion of forests dominated by red alder (*Alnus rubra*) to forests dominated by conifers, such as Douglas-fir (*Pseudotsuga menziesii*). Such changes in vegetation may impact subsidies of leaf litter inputs that fuel riparian food webs, yet there is little information on the rate and timing of energy and nutrient release associated with litter decay in these two riparian forest types. This study is designed to examine the influence of leaf litter characteristics and overstory species composition on decomposition patterns for both red alder and Douglas-fir litter, in the context of understanding how vegetation management could impact nutritional subsidies and nutrient cycles within these riparian systems.

Leaf litter breakdown is governed by complex interactions among chemical, physical, and microbial processes. The rate of leaf litter decay is affected by both internal factors of the litter—the chemical and physical qualities of the leaves themselves—and external environmental factors; moisture, temperature, and nitrogen (N) being the most important. In terrestrial environments, several aspects of leaf litter chemistry, such as the type of carbon compounds and nutrient concentrations, including the lignin:N ratio, have been correlated to decomposition rates and nutrient dynamics from species to species across a variety of systems. High quality litter like that from red alder has relatively low lignin:N ratios, decomposes rapidly, and quickly releases energy and nutrients. It has been proposed that this results in faster nutrient cycling and greater soil productivity. In contrast, litter of lower initial quality (higher lignin:N), such as Douglas-fir needles, decays more slowly, leading to lower nutrient cycling rates and soil fertility. Although these broad generalities have been developed by examining patterns of litter decay across species, there is little information on how variations in quality within a single species might influence decay rates.

In this study, we are examining the influence of litter source and riparian overstory composition on rates of leaf litter decay, both across species (red alder vs. Douglas-fir) and within a single species, Douglas-fir. We gathered litter from eight Douglas-fir stands across the Coast Range with known variations in foliar N, and are comparing decay of these varied Douglas-fir litters to the decay of red alder. Based on previous work in upland forests, we expect that red alder will decay more rapidly than Douglas-fir due to higher initial litter quality. Across the range of Douglas-fir litter sources, we expect more rapid decay of litter with a high initial N content. We also expect that environmental higher N availability will result in more rapid decay of litter in red alder than in Douglas-fir riparian sites. Similarly, N fertilization of Douglas-fir riparian sites is expected to stimulate rates of litter decay, particularly for the N-poor Douglas-fir litters.

METHODS

Decomposition of red alder and Douglas-fir leaf litter was measured by the litterbag method in which preweighed material was confined within mesh bags. Changes in mass, nutrient content, and carbon chemistry were measured over 2 years. Source litter samples were gathered during September and October 2003 by shaking branches of 20- to 35-year-old trees and collecting the resulting litter on tarps placed beneath the trees. Douglas-fir litter gathered from eight sites ranged in initial N concentration from 0.62% to 1.26%. Red alder litter was collected at a ninth collection site. The initial N concentration was typical for red alder leaves, 2.41%.

In total, 3,500 litterbags made of 1-mm nylon mesh were placed on the soil surface in November 2003. Three replicate bags for each collection were placed in one of two overstory habitat types, red alder or Douglas-fir, selected from a subset of sites studied previously by Emily Scott (2003 CFER Annual Report) in the central and southern Coast Range. There were four replications of each overstory type. At each Douglas-fir site, three additional replicate plots were added and fertilized monthly with N (as urea and ammonium nitrate) at a rate equivalent to 150 kg N / ha / yr, which is typical for N inputs under pure stands of red alder.

Ten replicate litterbags of each litter source (Table 1) were randomly placed in each plot for a total of 90 bags per plot. Replicate bags from each litter source were collected after 2 weeks, 1 month, 2 months, 4 months, 8 months, 1 year, 1.5 years and 2 years. Additional collections are scheduled for 3 and 4 years after initiation. At each collection, one replicate litterbag of each litter source was collected from each plot and weighed to determine mass loss.

Source	%N	%C	C:N	% Lignin	Lignin:N
Douglas-fir 1	0.62	51.17	82.59	34.97	56.45
Douglas-fir 2	0.722	52.56	72.8	30.11	41.7
Douglas-fir 3	0.892	53.12	59.55	29.21	32.75
Douglas-fir 4	0.916	52.16	56.95	28.88	31.53
Douglas-fir 5	0.931	52.78	56.69	34.87	37.45
Douglas-fir 6	0.996	52.41	52.65	33.97	34.12
Douglas-fir 7	1.163	53.43	45.96	33.02	28.4
Douglas-fir 8	1.264	53.51	42.33	34.6	27.37
Red alder	2.409	54.66	22.69	9.34	3.88

Table 1. Initial chemical characteristics of eight Douglas-fir needle litter sources and red alder leaf litter source.

We used both biomass remaining and integrated decay rate *k* (y^{-1}) to estimate decay after 2 years. Biomass remaining provides an estimate of overall litter decay, independent of the pattern of litter loss over time. In contrast, the integrated decay rate k provides an estimate of decay that incorporates variations in decay patterns over time. This approach can be useful where different litters produce single versus double exponential patterns of mass loss that are not directly comparable. The integrated decay rate k is calculated by estimating the area under the curves of mass loss versus time, using linear interpolation between collection points, calculating the area below this line, and summing the areas. We also used single and double exponential models to estimate decays rates of Douglas-fir and red alder, respectively.

Analysis of variance (ANOVA) was used to determine if there were significant differences in decay rates (i.e., biomass remaining and integrated k) between source litter and decomposition environments. Comparisons between red alder and Douglas-fir dominated sites were made using a completely randomized design. Comparisons between unfertilized Douglas-fir plots and fertilized Douglas-fir plots at Douglas-fir sites were made using a blocked design. Additionally, we compared red alder sites to fertilized Douglas-fir plots using a completely randomized design. Significant effects are reported at $\alpha = 0.05$.

Douglas-fir Decay

The decay constant, k (y^{-1}), is an integrated measure of the rate of decomposition (Olson 1963). To calculate k, I averaged the ratio of the mass at time of collection to the initial mass for the 3 plots at each red alder site, the 3 unfertilized Douglas-fir plots and the 3 fertilized Douglas-fir plots at each Douglas-fir site. This average was then log transformed and the slope of the regression line of mass versus time is defined as k (Olson 1963).

PRELIMINARY RESULTS

Red alder vs. Douglas-fir Leaf Litter Decay and N Dynamics

Initial leaf litter chemical characteristics varied widely among the Douglas-fir source litters, but the highest %N and lowest lignin:N ratio was observed in red alder litter (Table 1). To examine the rate and temporal nature of red alder leaves versus Douglas-fir needles, two out of the eight Douglas-fir litter sources--one low-N (Douglas-fir 1) and one high-N (Douglas-fir 7) were compared to the red alder leaf litter. Results of ANOVA, which included the three litter sources listed above, indicated that various source litters differed significantly in cumulative mass loss after 2 years in the field (Table 2 and Figure 1). Across all sites and fertilization treatments, the greatest cumulative mass loss occurred in the order: red alder > low-N Douglas-fir > high-N Douglas-fir (all statistically different at $p < 0.05$ when all models are considered concurrently). Across all sites and fertilization treatments, approximately 55% of red alder litter mass remained after two years, whereas low-N Douglas-fir litter averaged 60% mass remaining, and high-N Douglas-fir averaged 67% mass remaining. The site of decomposition (red alder versus Douglas-fir overstory) did not significantly affect cumulative mass loss after two years for all litter sources ($p = 0.45$) (Table 2). However, results show an interaction between source litters and fertilization of Douglas-fir sites ($p = 0.05$) (Table 2) with decreased mass loss resulting from N fertilization in Douglas-fir sites.

Model 1	**Percent Remaining**	**Integrated k**
Overstory ($F_{1,6}$, p)	0.64, 0.45	5.86, 0.05
Source ($F_{2,12}$, p)	7.21, 0.009	68.28, <.0001
Overstory*Source ($F_{2,12}$, p)	1.64, 0.23	6.18, 0.0143
Model 2		
DF Fertilization ($F_{1,3}$, p)	6.88, 0.08	0.34, 0.6214
Source ($F_{2,12}$, p)	10.58, 0.002	66.55, <.0001
DF Fertilization*Source ($F_{2,12}$, p)	0.05, 0.05	1.33, 0.2997
Model 3		
Added N ($F_{1,6}$, p)	5.01, 0.07	7.42, 0.03
Source ($F_{2,12}$, p)	9.06, 0.004	65.61, <0.0001
Added N*Source ($F_{2,12}$, p)	0.54, 0.59	2.77, 0.1027

Table 2. Analysis of Variance for percent biomass remaining and integrated k (y-1) values.

Note: Model 1 and 2 are comparisons using a completely randomized design between red alder and Douglas-fir overstories and red alder overstory and fertilized Douglas-fir treatments. Model 3 are results of comparisons between unfertilized and fertilized Douglas-fir plots under unfertilized Douglas-fir overstories. Variance estimates represent ad hoc variation from 4 overstory replicates and fertilization treatments.

Integrated decay rate "k"

Results of the ANOVA of integrated *k* showed an interaction between red alder leaf litter and red alder overstory with red alder decaying much more rapidly under red alder overstory than in either Douglas-fir overstories or fertilized Douglas-fir plots (p= 0.01) (Table 2 and Figure 2). Red alder leaf litter also decayed faster than either Douglas-fir litter source (Table 2) under all overstory and fertilization treatments. Across all sites and fertilization treatments, the value for integrated *k* was 0.29, 0.39, and 0.62 yr^{-1} for high-N Douglas-fir, low-N Douglas-fir and red alder leaf litter, respectively.

Red Alder Leaf Litter Decay

Red alder litter decay is characterized by rapid initial mass loss followed by a dramatic reduction in mass loss (Figure 1), characteristic of a double exponential model of decay. Multivariate analysis of variance (MANOVA) indicates that parameters from the double exponential model differed by overstory (red alder *vs*. Douglas-fir) ($F_{3,4}$ = 8.40, p = 0.03), but fertilization treatments had no effect on decay. In red alder sites, the fast pool composed 31.4% of total mass, with a decay rate (k_f) of 14.98 yr^{-1} (95% CI: 9.97, 19.97). The remainder of the mass decayed more slowly with a decay rate (k_s) of 0.22 yr^{-1} (95% CI: 0.15, 0.28). The fast pool of red alder was smaller in Douglas-fir sites, estimated at 22.5% of overall red alder mass, with k_f of 31.91 yr^{-1} (95% CI: 26.92, 36.89). The decay of the remainder of the mass, the slow pool, was 0.21 yr^{-1} (95% CI: 0.13, 0.27). Results from the double exponential found little evidence that the rate of decay for either pool is influenced by overstory (p=0.08) (red alder vs. Douglas-fir sites) or added N (p=0.07) (red alder sites vs. Douglas-fir plots).

Douglas-fir Needle Litter Decay

Results from ANOVA showed that decay rate of Douglas-fir litter sources differed, but overstory (red alder versus Douglas-fir sites) did not influence the rate of Douglas-fir source litters (p=0.54) (Tables 3 and 4). ANOVA results comparing Douglas-fir source litters and red alder overstory sites versus fertilized Douglas-fir sites showed an interaction between source and the fertilization treatment (p=0.05) with the difference between Douglas-fir litters depending on whether it was under red alder sites or fertilized Douglas-fir plots (Table 3). Within Douglas-fir sites, results showed that fertilization (p = 0.03) and source litter (p = 0.07) both influence the rate of decay, but there was no interaction between source and fertilization.

Although broad decay patterns of red alder versus Douglas-fir leaf litter followed expected trends, the results of examining leaf litter decay within Douglas-fir were highly unexpected. Specifically, decay of different Douglas-fir litter sources was related negatively to litter %N (Figure 3) and positively to lignin:N ratios.

Carbon and Nitrogen Dynamics

The pattern of net change in N concentrations and pools differed markedly between Douglas-fir and red alder litter (Figure 4). Douglas-fir litter immobilized N throughout 2 years of decay. After 2 years in the field, the concentrations of N decaying low-N Douglas-fir litter increased substantially, ranging from 124 - 190% of initial %N, with greatest N immobilization in red alder sites and fertilized Douglas-fir plots (Figure 3). High-N Douglas-fir litter showed similar trends, but immobilized less N overall, ranging from 100-122%

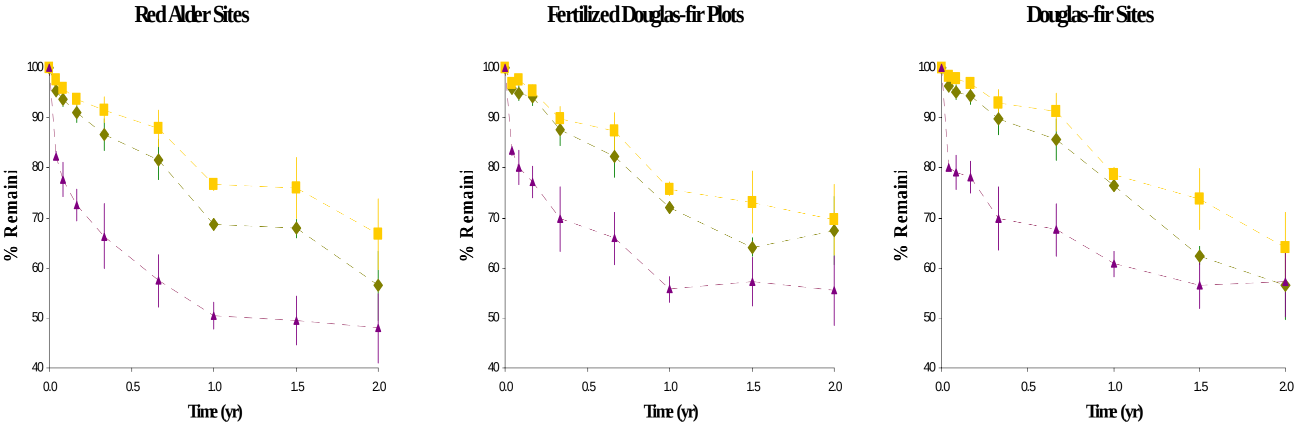

Figure 1. Biomass loss of red alder leaves and low- and high-N Douglas-fir needles in red alder and Douglas-fir overstories and fertilized Douglas-fir plots.

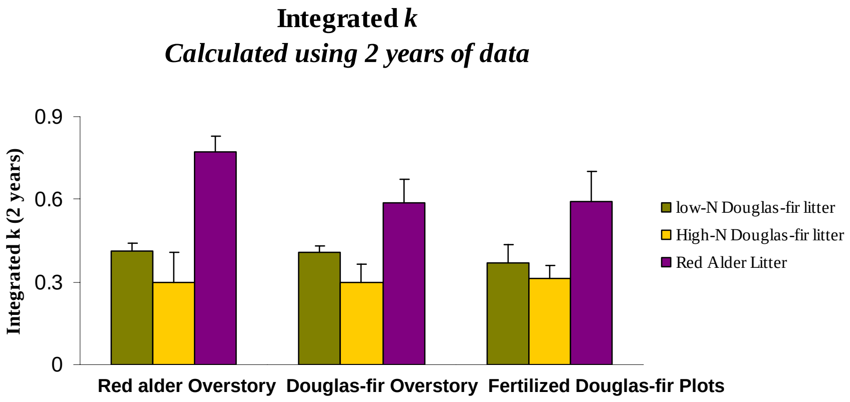

Figure 2. Integrated k results after 2 years for red alder leaves and low- and high-Douglas-fir needles under red alder and Douglas-fir needles under red alder and Douglas-fir overstories and fertilized Douglas-fir plots.

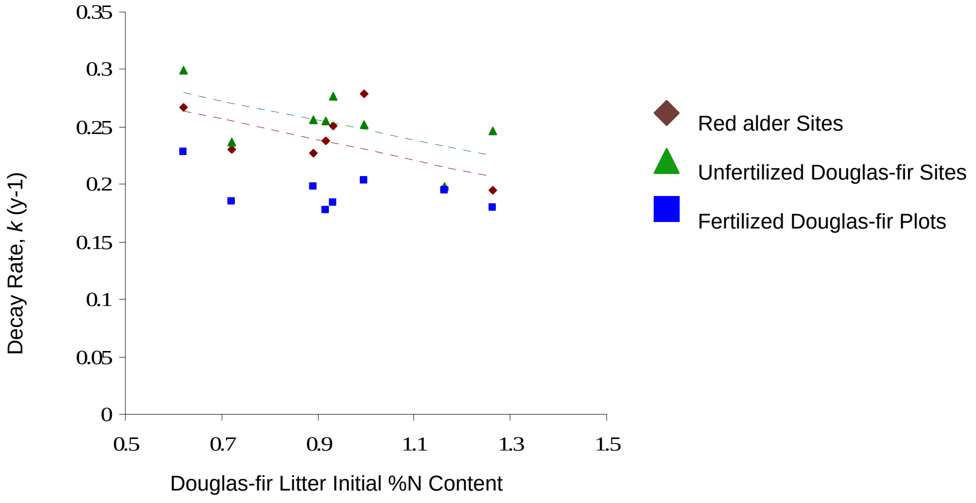

Figure 3. Relationships between % N content and *k* (y-1) of Douglas-fir litter sources in red alder and Douglas-fir sites and with fertilized Douglas-fir plots. Residual estimate error for regressions between initial N and Douglas-fir source litter between red alder and Douglas-fir overstory sites is 0.002. For comparisons between red alder overstory sites and fertilized Douglas-fir plots is 0.001.

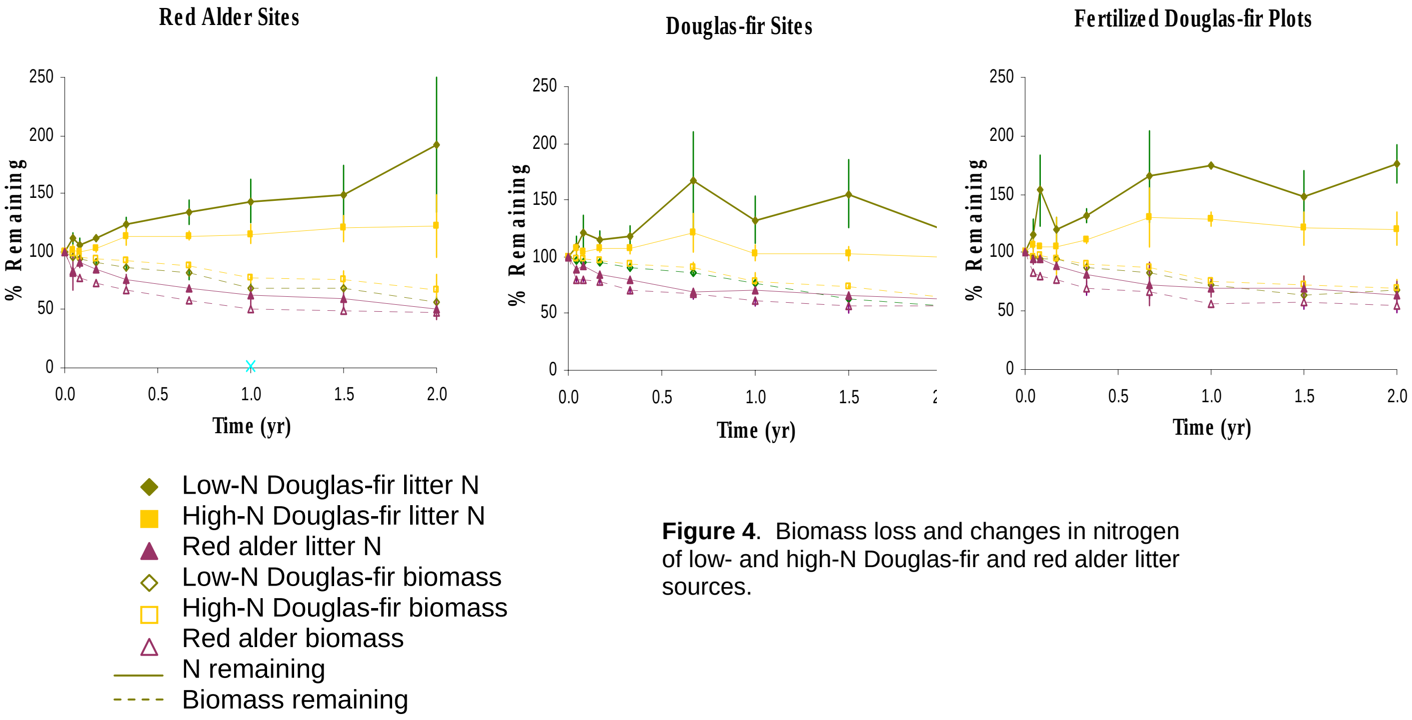

Figure 4. Biomass loss and changes in nitrogen of low- and high-N Douglas-fir and red alder litter sources.

Source Litter	Red Alder Sites	Douglas-fir Sites	Fertilized Douglas-fir Plots
DF1	**0.27** ±0.02	**0.30** ±0.02	**0.30** ±0.03
DF2	**0.23** ±0.01	**0.24** ±0.05	**0.19** ±0.04
DF3	**0.23** ±0.04	**0.26** ±0.05	**0.20** ±0.28
DF4	**0.24** ±0.08	**0.26** ±0.08	**0.18** ±0.24
DF5	**0.25** ±0.03	**0.28** ±0.08	**0.18** ±0.25
DF6	**0.28** ±0.05	**0.25** ±0.03	**0.20** ±0.28
DF7	**0.19** ±0.09	**0.20** ±0.06	**0.19** ±0.19
DF8	**0.19** ±0.05	**0.25** ±0.02	**0.18** ±0.20

Table 3. Data table of decay rate of various Douglas-fir litter sources under red alder and Douglas-fir overstory sites and fertilized Douglas-fir plots
Note: Standard error listed in table is an adhoc calculation from the 4 replicate sites of red alder and Douglas-fir overstories.

Model 1	***k* (y^{-1})**
Overstory ($F_{1,6}$, *p)*	0.45, 0.54
Source ($F_{7,42}$, *p*)	4.31, 0.01
Overstory*Source ($F_{7,42}$, *p*)	1.63, 0.15
Model 2	
Added N ($F_{1,6}$, *p)*	2.74, 0.15
Source ($F_{7,42}$, *p*)	3.39, 0.006
Added N*Source ($F_{7,42}$, *p*)	2.21, 0.05
Model 3	
DF Fertilization ($F_{1,3}$, *p)*	13.75, 0.03
Source ($F_{7,42}$, *p*)	2.08, 0.07
DF Fertilization*Source ($F_{7,42}$, *p*)	1.39, 0.24

Table 4. ANOVA results for comparisons of k (y-1) including eight Douglas-fir litter sources

of initial N. In contrast, red alder litter had no period of N immobilization. Instead, the loss of N from red alder litter paralleled organic matter loss (Figure 4), declining to 50-64% of initial N after 2 years. Red alder litter had no period of N immobilization, with N released to surrounding environment starting very early in the decay process and continuing throughout the 2 year period.

DISCUSSION

In Coast Range riparian forests, decay dynamics of red alder and Douglas-fir leaf litter differ in both the rate and temporal patterns. Red alder leaves can lose as much as 20% of their mass in the first two weeks of decomposition. Douglas-fir needles, in contrast, lose less than 5% of their biomass over the same period. After 2 years, red alder lost 45% of its mass, whereas Douglas-fir lost only 36% of its mass averaged across low and high N litter sources. Differences in integrated decay rates (Figure 2) support these species effects on biomass loss.

These stark differences in decay rates and patterns suggest that nutritional subsidies from red alder litter enter riparian food webs much more rapidly than Douglas-fir litter. The rapid decay of red alder litter, particularly when it occurs in steep riparian areas, may promote the transfer of nutritional subsidies from vegetation to terrestrial detrital food webs before the litter is removed by downslope movement to streams (Hart 2006, *Riparian Litter Inputs to Streams in the Oregon Coast Range*, 2006 CFER Annual Report). The slower decay of Douglas-fir, on the other hand, may allow a greater proportion of riparian vegetation nutritional inputs to reach streams, particularly on steep sites. Potential aquatic differences in red alder vs. Douglas-fir decay dynamics are being investigated in a companion study (see below). In addition to rapid mass loss, red alder leaves released available N to the environment from the onset of decay, while Douglas-fir litter sources continued immobilizing N even after two years, suggesting that red alder provides a rapid and near-continuous subsidy of nitrogen to food webs and growing vegetation in riparian areas. Collectively, this work suggests that red alder releases carbon, energy, and nitrogen more rapidly into food chains than does decomposing Douglas-fir.

A surprising result from our within species analysis was the negative correlation between initial source litter %N and decay rates of Douglas-fir litter. These surprising patterns stand in stark contrast to generally accepted conceptual models indicating faster decay at high %N and lower lignin:N ratio. Our results raise the possibility that traditional litter quality indices can predict decay rates effectively only for comparisons made across species (e.g., red alder vs. Douglas-fir). Traditional litter quality indices may not be sufficiently mechanistic to predict decay rate variations within species, and other unexplored factors of species identity may be as (or more) important than lignin and %N as predictors of leaf litter decay.

CONCLUSION

Differences in decay rates between red alder and Douglas-fir were consistent with comparisons of %N and lignin:N ratio predicted by standard conceptual models. The higher %N of red alder litter (2.4% N) in comparison to Douglas-fir (0.6–1.3% N), and the lower lignin:N ratio of red alder (lignin:N = 9) in comparison to Douglas-fir (range = 31–55) both indicate a higher litter quality for red alder. However, nitrogen additions did not stimulate decay rates as expected. To the contrary, nitrogen fertilization at a rate typical of red alder N fixation decreased the decay of

Douglas-fir, particularly for N-rich litter. This decrease in Douglas-fir decay rate may have arisen due to nitrogen inhibition of enzymes responsible for lignin degradation, as has been reported in decay studies of other high-lignin species under N-rich conditions. In addition, Douglas-fir litter did not decay more rapidly in red alder dominated riparian areas relative to rates observed under Douglas-fir overstory. Thus, the positive nutritional effect of including red alder in Douglas-fir dominated riparian forests is likely to be limited to the direct effects of red alder litter inputs, with less of an impact on the decomposability of Douglas-fir litter. On the other hand, red alder litter did decay more rapidly under red alder overstory, but not in response to N fertilization, suggesting that other factors associated with red alder forests, such as soil invertebrate and microbial food webs may also influence decay rates. Maintenance of red alder in riparian forest habitats may therefore be desirable to sustain energy, carbon, and nutrient cycling that otherwise could limit food resource availability to consumer organisms.

Aquatic Component Update

The aquatic component of this research was initiated in September 2004. The aquatic experiment used the same litter sources and litterbag methods described above. On the basis of other research showing correlations between dissolved N concentrations in stream water and the amount of red alder in the watershed, we selected study sites to span a range of aquatic N levels as indexed by the percentage of watershed area dominated by red alder. Water samples were subsequently taken and tested for ammonium, nitrate, and total dissolved N concentrations. We established eight aquatic sites; four with high stream water N and four with low stream water N. Litterbags from this experiment were collected 1 day after initiation to evaluate a 24-hour leaching period. Subsequently, collections were conducted after 1 week, 2 weeks, 1 month, 2 months, 3 months, 4 months, and 5 months, with the last collection in February 2005.

STUDY TIMELINE

The terrestrial experiment was initiated November 2003. Data collection for a graduate student thesis will continue through November 2006 with additional collections in November 2007. The aquatic experiment was initiated September 2004. Data collection was completed in February 2005. Lab work began during spring 2004. Data analysis and thesis writing will occur during the fall of 2006.

Reference

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44: 322-331.

The Cooperative Forest Ecosystem Research (CFER) program was developed to facilitate sound management of forest ecosystems, with emphasis on meeting priority research information needs of the Bureau of Land Management (BLM) and the Oregon Department of Forestry (ODF) in Western Oregon.

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