An Abstract of the Thesis of

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The effects of initial leaf litter chemistry of 16 common coniferous and deciduous hardwoods and shrubs on their annual decomposition patterns were studied on the H.J. Andrews Experimental Forest (Oregon). Leaf litters were characterized by their chemical qualities, which included measurement of elemental fractions (C, N, P, K , Ca, Mg), proximate fractions (non-polar, polar, acid-soluble extractives, acid-soluble lignin and acid-insoluble "Klason lignin"), and colorimetric characters (total phenolics, reactive polyphenolics, water-soluble carbohydrates, water-soluble condensed tannins, and water and acid-insoluble condensed tannins). These analytical methods improve upon traditional proximate analysis (Ryan et al. 1990) used to characterize leaf litters, through measurement of reactive and residual phenolic fractions and acid-soluble lignin. This paper discusses the procedures that are involved in improving proximate analysis and the link between leaf chemistry and one year decomposition rates.

Significant differences were found in leaf litter qualities and in decomposition rates (expressed as decay) among species. The annual decay (k) for the leaf litter ranged from 0.27 to 1.02. The decay values for all species combined had highly significant ($p \leq 0.0001$) correlations with 29 out of the 36 initial chemistry variables tested. The three highest correlations were with acid-insoluble condensed tannins (r= 0.83 $p \leq 0.0001$ n= 339), the lignocellulose index (r= -0.81 $p \leq 0.0001$, n=339) and acid-insoluble residue or "Klason lignin" (r= -0.80 $p \leq 0.0001$, n=339). A multiple regression model with all 16 species suggested that annual decomposition was best related to acid-insoluble condensed tannins, Klason lignin, water-insoluble condensed tannins, Ca and total phenolic:N (R^2=0.84, $p \leq 0.0001$, n= 339). Correlation and multiple linear regression models with each species' decay rate revealed that no one single initial chemical predictor could best explain the decomposition rates for each of the 16 species and that there were a wide range of chemical predictors related to the patterns of decomposition for each species.

Master of Science thesis of Yana S. Valachovic presented on April 10, 1998

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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.

Yana S. Valachovic

Yana S. Valachovic, Author

Leaf Litter Chemistry and Decomposition in a Pacific Northwest Coniferous Forest Ecosystem

by

Yana S. Valachovic

A THESIS

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Contribution of Authors

Bruce Caldwell, Dr. Kermit Cromack, Jr. and Dr. Robert P. Griffiths were involved in the design of the project. Bruce Caldwell was involved with the sample collection, chemical analysis, and interpretation of the data. The assays were preformed in the laboratory of Dr. Robert P. Griffiths.

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Leaf Litter Chemistry and Decomposition in a Pacific Northwest Coniferous Forest Ecosystem

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Introduction

The decomposition of leaf and needle litter fall is a critical part of forest nutrient cycling processes (Swift et al 1979, Cadisch and Giller 1997). Numerous studies have attempted to predict litter decomposition rates using a wide range of initial leaf litter quality characters (see Table 1), e.g., lignin (Peevy and Norman 1948, Fogel and Cromack 1977), nitrogen (Bosatta and Staff 1982), lignin to nitrogen ratios (Mellilo et al. 1982, Harmon et. al. 1990). Of these, a great majority have focused on lignin or nitrogen control of decomposition rates, while only a few studies have considered the potential influence of reactive polyphenols (synonym "tannins") on decomposition rates (Palm and Sanchez 1991, Gallardo and Merino 1992, Tian et al. 1992).

Polyphenols are aromatic compounds that possess two or more hydroxyl (OH) substituents. Woody plants contain both low molecular (e.g. catechol and phenolic acids) and high molecular phenolics. Higher molecular phenols can be oligomeric or polymeric and include tannins. There are two general types of tannins, hydrolyzable tannins (a sugar core onto which a gallic acid is linked by esterification) and condensed tannins (flavonoid polymers) (Waterman and Mole 1994). Both types of tannins are water-soluble phenolic compounds and have the ability to form hydrophobic or hydrogen-bonded complexes (Loomis and Battaile 1966, Oh et al. 1980, McManus et al. 1981, 1985, Nyman 1985) with detrital proteins, nucleic acids, polysaccharides and phospholipids (Handley 1954, Lewis and Starkey 1968, Takechi and Tanaka 1987, Mole and Waterman 1987, Haslam 1989, Zucker 1993). These

complexed substrates are resistant to hydrolytic enzymes (Handley 1961, Basaraba and Starkey 1966, Benoit et al. 1968, Lewis and Starkey 1968, Zucker 1983) and are thought to slow decomposition, leading to organic matter accumulation in acidic forest soils (Handley 1954, 1961, Basaraba and Starkey 1966, Gosz 1981, Zucker 1983, Harborne 1997). Tannins are found in the plant cell wall (Zucker 1983), within the central vacuole and subcellular organelles (Stafford 1988), where, upon cell death, they can easily react with cytoplasmic proteins and nucleic acids.

Lignins by comparison are random polymers of phenylpropyl units and are found only in plant cell walls. Lignins, however, do not appear to have any direct mechanisms to react with energy rich detrital compounds containing N or P and their location in the cell wall appears to further reduce the likelihood of direct interaction with the cytoplasmic proteins and nucleic acids. Lignins are thought to influence decomposition processes and to be difficult to degrade for a variety of reasons; first, within the cell wall, they act as barriers preventing decomposing organisms access to the cytoplasm; second, their polymers are very large and highly branched, which makes them susceptible only to extracellular enzymes; third, because lignins have an irregular stereochemistry requires that lingnolytic enzymes be less specific and as a result are less efficient than most biological enzymes; and forth, lignins are insoluble in water, making their decomposition controlled primarily by the availability of lingnolytic enzymes (Hammel 1997).

Consequently, the mechanism of polyphenol reactivity is more likely to control decomposition rates than lignin. There has been considerable interest in the role that polyphenolics may have in decomposition process (Vallis and Jones 1973, Zucker 1983, Horner et al. 1988, Palm and Sanchez 1991, Gallardo and Merino 1992, Tian et al. 1992), however no previous litter decomposition study has measured and tested actual polyphenol reactivity in relation to decomposition processes. Additionally, leaf litter decomposition studies have also been limited in that only a few species have been studied (see Table 1) and that they typically measure only a few indicators of litter quality, such as C, N or lignin (Pinck et al. 1950, Fogel and Cromack 1977, Meentemeyer 1978, Melillo et al. 1982, Scott and Binkley 1997).

Testing the influence of reactive polyhenols (RPP's) and lignin on leaf litter decomposition required an evaluation of conventional litter analyses known as proximate analysis. This evaluation was warranted because conventional procedures often underestimate polyphenolic concentrations and overestimate the lignin fraction (Reed et al 1982, Haslam 1989, Hammel 1997, Preston et al. 1997). Proximate analysis (Ryan et al. 1990) includes measurement of non-polar extractives (NPE) consisting of leaf fats, waxes and oils; polar extractives (PE) consisting of water-soluble sugars, polysaccharides, phenolics and tannins; acid-solubles (AS) consisting of cellulose and hemicellulose; and acid-insolubles (AI) a residue consisting of lignin, waxes, insoluble polyphenolics (as condensed tannins) and minerals generally termed

"Klason lignin" (Waksman et al. 1928, Preston et al. 1997). In this conventional procedure lignin is only functionally defined but is not actually measured. Furthermore, current proximate analysis does not account for acid-soluble lignins which can represent significant fractions of the total lignin in deciduous wood and litter (Lai and Sarkanen 1971, Effland 1977, Hammel 1997). These procedures also ignore many other important compounds, such as the chemical reactivity of phenolics, and water-insoluble and acid-insoluble condensed tannins and cutin.

Improvements in the proximate litter analysis were hypothesized to significantly improve decomposition predictability, first by more accurately measuring the lignin and phenolic pools, and secondly by exploring the reactivity of polyphenolics as a mechanisms to explain decomposition patterns. There were two objectives of this project: first to expand the traditional proximate leaf analysis (Ryan et. al. 1990) to include measurements of reactive polyphenols, water and acid-insoluble condensed tannins, acid-soluble lignin, acid-insoluble lignin, cutin and residual mineral fractions; second to test the improved leaf litter analyses in a one year litter decomposition model using a range of common Oregon tree and shrub species. These objectives include testing the following questions.

1. Are there differences in decomposition rates between species?
2. Are there differences in litter chemistries between species?
3. What individual initial litter quality measurement best predicts decomposition for each species separately and for all 16 species together?
4. What set of initial litter qualities measurements best predicts decomposition for each species separately and for all 16 species together?
5. How does the improved proximate analysis, including measurement of reactive polyphenolics, traditional proximate analyses, and commonly used predictors perform in predicting decomposition for a range of Oregon litter types?

Table 1. Demonstrated associations between initial litter quality and decomposition processes.

Predictor	Species Type[1]	Species Total	% Lignin	% N	Reference
N	ND	ND	ND	ND	Bosatta &Staff, 1982
	1	1	ND	0.42-2.51	McClaugherty & Berg, 1987
	1, 2	2	~10-22	0.88-2.2	Flanagan & Van Cleve, 1983
	1	2	22-31.7	0.4-1.3	Chadwick et al., 1998
C:N	2,4	11	5.3-21.9	0.4-15.6	Pinck et al., 1950
	1,2	14	3.9-31.0	0.9-1.2	Cromack and Monk, 1975
	1,2,5	4	ND	0.45-1.52	Edmonds, 1980
	1,2,3,4	8	3.4-20.5	0.52-1.31	Taylor et al., 1989
Lignin	4,5	3	3.4-26.3	0.05-3.54	Peevy and Norman, 1948
	1,6	1	21.8-58.6	0.15-0.82	Fogel and Cromack, 1977
	1,2	ND	13.6-29.1	ND	Meentemeyer, 1978
	1, 2	7	5.3-22.4	0.42-2.20	White et al., 1988
	1,2	10	5.8-23.4	0.52-1.32	Upadhyay et al., 1989
	2	4	9-40	0.4-1.4	Cortez et al., 1996
Lignin:N	2	6	10.1-24.1	0.6-1.2	Mellilo et al., 1982
	1,2,5	10	2.7-27.9	0.30-2.20	Harmon et al., 1990
	1,2	4	19.4-26.5	0.45-0.73	Stump and Binkley, 1993
	1,2	12	ND	ND	Cornelissen, 1996
	2,4	5	10.8-49.1	0.63-1.7	Hobbie, 1996
	ND	ND	5.6-30.8	0.47-2.34	Aerts, 1997
Lignin:N_{min}	1,2	>30	6.7-29.3	0.38-1.4	Scott and Binkley, 1997
N+ Lignin	2	9	16.1-20.7	0.69-0.91	Boerner, 1984
Lignin+N	1,2	6	2.0-13.8	0.83-2.56	Pandey and Singh, 1982
Lignocellulose	1	1	ND	ND	Mellilo et al., 1989
Lignin + Hollocellulose	1	1	22.3-25.7	3.8-4.1	Berg and Agren, 1984
Cellulose+ Hemicellulose	1	1	21.9-34.8	0.3-0.47	Johansson, 1994
PP	3,5	2	3.1-15.6	1.9-5.0	Vallis and Jones, 1973
	2,4	5	5.2-47.6	0.12-3.6	Tian et al., 1992
PP_{Nimm}	2	9	8.9-20.2	0.33-0.93	Gallardo and Merino, 1992
PP:N	4	4	ND	0.05-0.1	Aerts and de Caluwe, 1997
PP:N_{min}	2,3,4,5	11	5.2-17.9	1.13-3.94	Palm and Sanchez, 1991
(Lignin+PP):N_{Min}	5	6	4.2-11.1	1.7-4.6	Fox et al., 1990

ND- No Details given
N Min= as measured by N mineralization
N Imm=as measured by N immobilization
PP- Total Phenolics
Hollocellulose= cellulose + hemicellulose
1. Species type is 1= conifers, 2= hardwoods & shrubs, 3=herbs, 4= grass, 5= N fixers, 6= woody material

Methods

Leaf Collection

Leaf material from 16 species (Table 2) was collected from a range of locations across western Oregon during the Fall of 1995. These species were chosen because of their anticipated range in chemical qualities, e.g. lignin, nitrogen, and phenolic fractions (Nilsson et al. 1998). Leaf material was collected that had recently senesced or that could be gently shaken free on to tarpaulins. Each species litter was collected from 5 different sites. The leaf material was air-dried to a constant weight in a laboratory at Oregon State University. A 30 gram (g) sample was ground with a Wiley mill (40 mesh) for chemical analysis.

Decomposition Experiment

Litterbags with 5 g of leaf material were made from leaf litter collected at each site. There were 3-5 replicate litterbags made from each collection site or 15-25 litterbags per species (see Table 2.). Litterbags were made of 1 mm nylon mesh bags and were 20 x 20 cm in size. The fine conifer litter from *Douglas-fir* and *Pacific silver fir* were placed in a litterbag two layers thick to insure needle retention. The litterbags for all species were assigned at random across an area of approximately 36 x 22 meters within one forested stand (44° 12' 54" N latitude and 122° 14' 57" W longitude) in the Cascade Mountains at the H. J. Andrew Experimental Forest on November 18, 1995. The site was a

mesic old-growth forest with an overstory of Douglas-fir and Western hemlock trees around 460 years old. The habitat type is classified as western hemlock/ sword fern/ Oregon oxalis. The mean annual temperature was 9.6° C (range 4.9° to 14.3° C) and the mean annual precipitation, mostly as rain, is 1869 mm. The elevation is 485 meters. The soils have been described as fine-loamy, mixed frigid family of Dystric Eutrocrepts (Brown and Parsons n.d.). The litterbags were placed on the forest floor and were secured with a pin flag. Litterbags were collected after one year and dried, cleaned and reweighed. Decomposition was measured as weight loss of the leaf material over one year and was expressed as decay. The decay constant (k) was calculated using the equation $\ln(Xt/Xo)= -kt$, where Xo is the original weight of the litter in the bags and Xt is the weight of the litter after time t (years) (Olsen 1963). Solving this equation requires taking the negative natural log of the % mass remaining for each litterbag.

An air-dry versus oven-dry (50° C for 8 hours) test confirmed that the average difference in weight between the two forms of drying was approximately 5%. An additional test confirmed that the average loss associated with transport of the litterbags to and from the field was 1.2% (0.5-3.4 % range). Because these differences in weights were so small they were not corrected for in the decay values.

Table 2. Common and scientific names for each species and the number of litterbags constructed for the decomposition experiment.

Species	Scientific Name	# of litter bags
Conifers		
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco	15
Pacific silver fir	*Abies amabilis* (Dougl.) Forbes	25
ponderosa pine	*Pinus ponderosa* Dougl. ex Loud.	25
western redcedar	*Thuja plicata* Donn.	25
Hardwoods		
bigleaf maple *	*Acer macrophyllum* Pursh	15
golden chinkapin	*Castanopsis chrysophylla* (Dougl.) A.DC	25
Oregon white oak *	*Quercus garryana* Dougl.	15
Pacific dogwood *	*Cornus nuttalli* Aud. ex T. & G.	25
Pacific madrone	*Arbutus menziesii* Pursh.	25
poplar *	*Populus trichocarpa* T. & G.	15
salal	*Gaultheria shallon* Pursh	25
red alder §*	*Alnus rubra* Bong.	15
snowbrush §*	*Ceanothus velutinus* Dougl. Ex Hook.	25
rhododendron	*Rhododendron macrophyllum* G. Don	25
Sitka alder §*	*Alnus sinuata* (Reg.) Rydb.	25
vine maple*	*Acer circinatum* Pursh	25

§ = nitrogen fixing species
* = deciduous species

Litter Quality Analysis

Analysis of Inorganic Fractions

Subsamples (0.3 gram each) of the ground material were oven-dried (50° C), C and N was determined by a Leco CNS Analyzer, and P, K, Mg and Ca were measured by auto analyzer (ALPKEM RFA) following a Kjedal digestion (Thomas et al. 1967). Another 1 g subsample was ignited in a muffle furnace at 550° C overnight to determine the ash fraction. Note, the grinding

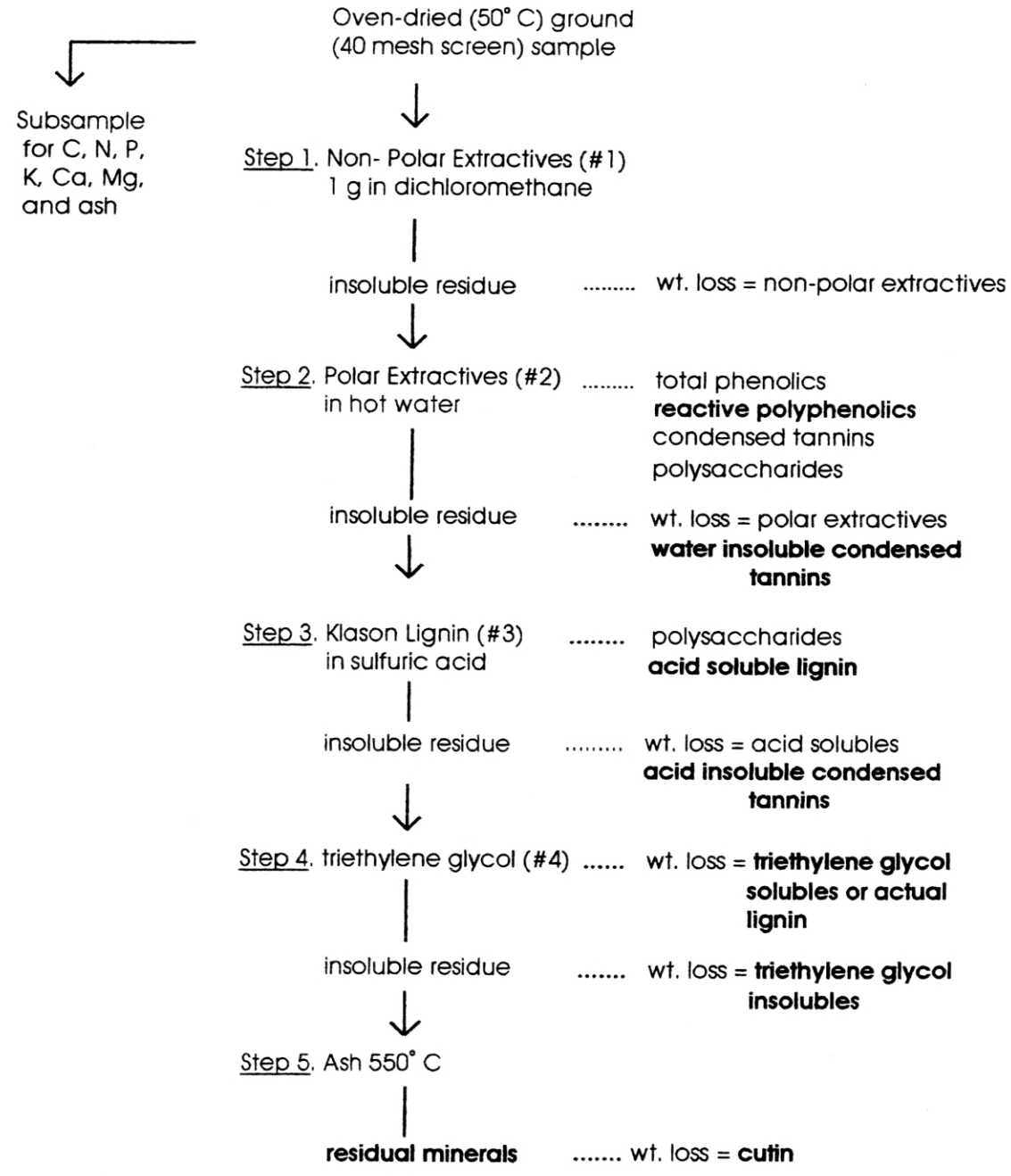
size was found to influence the analytical results and a 40 mesh size is preferable over 20 mesh.

Analysis of Organic Fractions

A 1 g sample of the ground material was sequentially extracted, adapting methods from Ryan et al. 1990 (sequences displayed in Figure 1). Each sample was run in duplicate through the all the litter quality analyses and averaged.

Step 1: Non-Polar Extractives: One g of oven-dried (4 hrs at 50° C) leaf material was placed in an oven-dried and preweighed 30 mL Gooch crucible within a 100 mL beaker . The sample was sonicated with 30 mLs of dicholoromethane for 30 minutes. The filtrate was removed with light suction and washed with 10 mL of dichloromethane. The procedure was repeated three times. The crucible with the pellet was air dried for 1 hour and oven-dried at 50° C for 4 hours. The crucible was weighed and stored in a desiccator until the polar extractive procedure. The use of a desiccator is critical because the pellet easily absorbs moisture from the room and adds weight. The amount of material lost in this procedure was the non-polar extractive fraction.

Figure 1. Sequential extraction diagram for the leaf chemical analyses.



There are five steps in the gravimetric analysis of the leaf material. On the right are the gravimetric and colorimetric fractions measured at each step. The compounds in **bold** are the additions to the proximate analysis scheme (Ryan et al. 1990). The numbers in parenthesis refer to the crucible used at each step.

Step 2: Polar Extractives: The NPE pellet was scraped out of the first crucible with a rubber spatula, was weighed and placed into a large centrifuge tube. Care was taken not to damage the crucible frit so as not to add weight to the next fraction. Twenty-five mLs of DI water were added to the tube, the tube was sealed with aluminum foil and vortexed, and was placed into a steamer for 1 hour. After being steamed, the tube is centrifuged for 10 minutes at 2,500 RPMs. The filtrate was suctioned off with a Pasteur pipette into a Ehrlenmeyer flask. The procedure was repeated three times. After the third steaming the filtrate and the pellet in the tube was filtered through a new oven-dried and weighed Gooch crucible, was oven-dried at 50° C for 4 hours and weighed. The filtrate was then transferred to volumetric flasks and brought up to 300 mL volume with DI water. A 50 mL subsample of the filtrate was stored frozen immediately after completing the procedure in labeled plastic screw-top bottles to be used for the colorimetric procedures described below. The amount of material lost in the extraction was the polar extractive fraction.

Initially four solvents were compared on 100 mg of the NPE pellets from bigleaf maple, Douglas-fir, Oregon white oak, poplar, and red alder: 70% aqueous acetone (Hagerman 1988) with sonication, or 50% aqueous methanol (Gray 1978) with sonication, or a one hour steaming with DI water (Ryan et al. 1990), or three one hour DI water steamings. No significant difference between the three one hour water steaming and the 70% aqueous acetone extraction was found in recovery of water-soluble total phenolics using catechol as a

standard (Julkunen-Tiitto 1985), and condensed tannins (Porter 1986) using commercial cyanidin (Wacko Chemical LTD) as a standard. The three one hour steaming was chosen because it was easier to work with than the 70% aqueous acetone and would be a better solvent for polysaccharides.

Step 3: Klason Lignin: The entire weighed PE pellet (generally under 600 mg) was scraped out of the second crucible into large screw top test tubes and weighed. Six mL of 72% sulfuric acid was added to the tube, the tube was vortexed and was placed into a 30° C water bath for an hour (vortexing every 15 minutes). At the end of the hour, 18 mL of DI water was added to the test tubes. The pellet and the water was then transferred to a 250 mL Ehrlenmeyer flask using 150 mL DI water to transfer the material. The Ehrlenmeyer was capped with aluminum foil and autoclaved for one hour. The flasks were cooled and filtered through a new crucible and brought up to 300 mL in volumetric flasks with DI water. A 10 mL subsample of the filtrate was immediately stored frozen in scintillation vials for analysis of acid-soluble sugars and lignin. The amount of material lost in the extraction was referred to as the acid-soluble fraction and the residual material as the acid-insoluble fraction or "Klason lignin". Note, the total volumes can be adjusted as long the ratio of 1 mL of 72% H_2SO_4: 1 g of plant material and a 28 mL DI:1 mL H_2SO_4 is maintained in the secondary hydrolysis.

Step 4 and 5 Cutin and Ash: The remaining AI pellet (which is generally under 250 mg) was weighed and added to a large screw-top test tube. Ten mL of activated triethylene glycol (TEG) (3.2 mL of 37% HCl and 500 mL triethylene glycol) was pipetted into the tube, the tubes were capped, vortexed, and autoclaved for one hour at 121° C (Edwards 1973). After cooling, the tubes were vortexed again. Edwards (1973) used three washes of 10 mL 95% EtOH to rinse the tube through a Gooch crucible under light suction, followed by 2 washes of 10 mL acetone, however this was found to not be sufficient to removed the triethylene glycol and required several more washes until the crucible was visibly clean. The crucible and the residue were dried and weighed. The crucible with residue was then ashed in a muffle furnace 550° C over night, to determine "cutin" by mass loss and the insoluble mineral fraction. The amount of material lost was the TEG soluble fraction. There was a problem in this step because of the size of the AI pellet and the difficulty in washing the TEG residues off the crucible. The procedure seems to work better with a larger starting material.

Colorimetric Techniques

Figure 1 displays when each of these colorimetric assays are used in the sequential scheme. Except for the water and acid-insoluble condensed tannin assays, a water blank was used to compensate for the absorbance of the filtrate in all of the assays described below.

- **Total phenolics** in diluted (1:10) hot water filtrate were determined with the Folin-Ciocalteau colorimetric reaction (Julkunen-Tiitto 1985) using catechol (1,2-dihydroxybenzene) as a standard. Commonly total phenolics are measured using tannic acid as a standard (Gallardo and Merino 1992 and 1993), but this is not actually a measurement of tannins or proanthocyanidins.
- **Reactive polyphenolics** were determined by shaking 3 mL of the diluted hot water filtrate and with 150 mg casein powder for three hours (Kuiters 1987). The solution is centrifuged and the supernatant is assayed for total phenolics. The difference between the pre-casein and post-casein values is the reactive phenolic portion and shows the ability of the phenolics to bind with a protein.
- **Water-soluble condensed tannins** (or proanthocyanidins) in hot water filtrate were determined with the butanol- HCl colorimetric reaction (Porter 1986) at 520 nm. Hydrolysis was carried out in the steamer instead of a water bath. Even heating between the tubes is very important in this assay as well as the choice of a standard.
- **Water-insoluble and acid-insoluble condensed tannins** were measured using Porter's (1986) and Reed's (1986) methods on 30-50 mg of the water and acid extraction pellets.

- **Water-soluble sugars** in diluted (1:10) hot water filtrate were determined with the phenol-sulfuric acid colorimetric reaction using a glucose standard (Dubois et al. 1956).
- **Acid-soluble sugars** in diluted (1:10) acid filtrate from the lignin procedure were determined with the Dubois et al. (1956) method.
- **Acid-soluble lignin** in diluted (1:10) acid filtrate was determined by absorbance at 205 nm in a quartz cuvette (Wood and Kellog 1988).

Predictor Methodology

The literature was reviewed for factors predicting leaf litter decomposition rates. In addition to the predictors displayed in Table 1, several other variables were found to predict decomposition processes. These include P, C:P (Schlesinger and Hasey 1981), total phenolics:P, lignin:P, N:P (Aerts and de Caluwe 1997) and the total phenolics: water-soluble carbohydrates and lignin: water-soluble carbohydrates (Entry et al. 1992). In this study, there was interest in finding the best predictor/s of decomposition both for individual species and for groups of species. In all, 36 independent variables were assessed for their predictive abilities including variables from standard proximate analysis, our additions to proximate analyses, and variables reported to predict litter decomposition rates by others.

Statistical Techniques

All of the analyses were preformed in SAS version 6.12 (1994).

1. To test for differences in decomposition rates between species, one-way analysis of variance (ANOVA) was used at $p \leq 0.05$ to analyze the effect of species on annual decomposition rates.

2. To test for differences in 36 litter chemistries between species, one-way ANOVA at $p \leq 0.05$ was used to analyze the effect of species on litter chemistry. Individual chemistry means between species were compared using Fischer's Least Significant Difference (LSD) at $p \leq 0.05$. The coefficient of variation was used to show how much variation was associated with each chemical fraction for each species.

3. To find which individual litter quality measurement best predicts decomposition for the decay values (k) of each species separately and for the decay values of all species together, correlation analysis was used. Residual analysis indicated that the assumption of constant and homogenous variance were met and no influential outliers were present in the data sets. Correlation analysis was used to find the linear relationships between the 36 possible predictors of the annual decay rates (k). The 36 possible predictors were sorted and ranked based on their r and p-value from the correlation analysis. The ranking showed which variables were strongly and weakly related to the annual decay rate for all the species together in one model and for each individual species separately.

4. To find which **set** of individual litter quality measurements best predicts decomposition for the decay values (k) of each species separately and for the decay values of all species together, multiple linear regression and Principle Components Analysis (PCA) (SAS 1989) were used. A correlation matrix was used to see if there were relationships between the independent variables, and significant ($p \leq 0.05$) correlations were found. This presents a small problem for multiple regression analysis because the assumption of true independence cannot be met (Ramsey and Schafer 1997). Step-wise model selection was used, with a minimum significance for entry into the model and to stay in the model at $p \leq 0.05$ for the multiple regression analysis. The step-wise model selection was chosen because it is the best combination of forward and backward model selection. However, step-wise selection did allow for some collinearity to remain in the models ($r=0.7$) and because of this collinearity we caution against traditional interpretation of the coefficients. PCA was used as an alternative method to the multiple regression model selections and to help with the collinearity in the all-species model. PCA was warranted because it creates linear combinations of the variables that are independent of each other and these combinations reflects which variables explain the overall variation in the data set .

5. To assess how the improvements in chemistry preformed in predicting decomposition, the results from questions three and four were evaluated.

Results

Decomposition Experiment

There were significant differences in decay rates between species ($p < 0.0001$). The annual decay rate was highest, indicating more rapid decomposition for two species, dogwood (k= 1.02) and vine maple (k= 0.82) and was generally lowest for the slower to decompose conifers. The species could be grouped by their decay rate representing four different types of species physiology, e.g. nitrogen fixers, conifers, hardwoods and rapid decomposers. For example (as shown in Figure 2), following vine maple and dogwood in decay rate were the three nitrogen fixers; red alder, Sitka alder and snowbrush. The conifers (on the slow end) were all tightly grouped except for Pacific silver fir (k=0.36) which was close to the median in decay rate and fell within the hardwood group.

Litter Quality Analytical Methodology

Although reactive polyphenolics, insoluble condensed tannin fractions, and the acid-soluble lignin fractions for all species were detected, problems prevented accurate extraction of the acid-insoluble residue or the "Klason lignin" pellet with triethylene glycol.

Problems were also encountered with finding an appropriate standard for the proanthocyanidin assay for condensed tannins. An attempt was made to use a commercial cyanidin but the absorbancies of the standard curve were

too low so the published extinction coefficient of 150 (Bate-Smith 1973) was used to calculate % condensed tannin per gram sample. C. M. Preston (per. comm.) recommends using a purified tannin standard from each specific litter type.

Litter Quality Analysis

Species means, standard errors (SE) and coefficient of variations (CV) for elemental analysis, proximate analysis, colorimetric analysis, and from predictive indices are displayed in Tables 3-6 respectively. The data are displayed based on the 4 groupings of tree physiology, i.e. nitrogen fixers, conifers, hardwoods and rapid decomposers. For each independent variable, the results of the ANOVA analysis showed significant differences in the mean values between species (p <0.0001). In Tables 3-6, the least significant differences (LSD) can be used to estimate statistically significant (p< 0.05) differences between species means. The CV shows the amount of variation within a species collection.

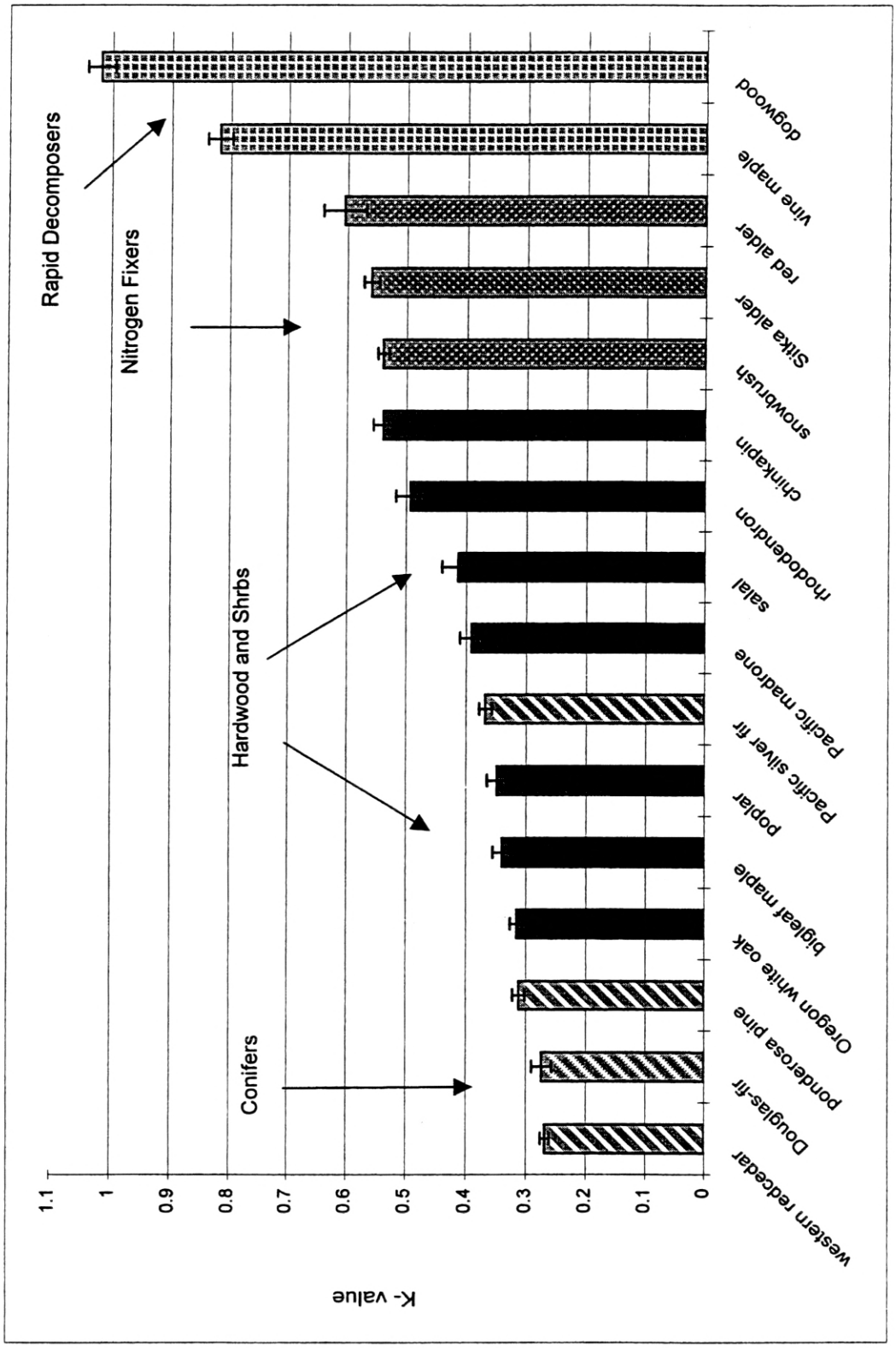


Figure 2. Mean annual decay rate (k) for each species (error bars= 1 standard error).

Table 3. Elemental analysis of leaf litter chemistry for each species (n= 5).

Group	Species	% Carbon			% Nitrogen			Phosphorous			Calcium			Potassium			Magnesium		
								mg.g^{-1}											
		mean	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV
1	*red alder*	**50.00**	0.12	0.53	**2.13**	0.12	12.91	**1.08**	0.08	16.61	**9.87**	0.83	18.84	**7.23**	0.39	12.13	**2.14**	0.18	18.34
1	*Sitka alder*	**49.88**	0.14	0.61	**2.44**	0.06	5.25	**1.83**	0.14	17.50	**10.89**	0.95	19.50	**3.30**	0.17	11.18	**2.60**	0.26	22.28
1	*snowbrush*	**53.02**	0.23	0.97	**1.40**	0.09	15.13	**0.80**	0.07	20.24	**9.19**	1.22	29.76	**5.51**	0.57	23.32	**1.61**	0.22	30.06
2	*Douglas-fir*	**51.62**	0.07	0.32	**0.52**	0.02	6.83	**0.70**	0.03	9.08	**10.89**	0.30	6.12	**0.56**	0.12	47.20	**0.92**	0.13	31.41
2	*Pacific silver fir*	**51.92**	0.29	1.24	**0.37**	0.02	14.80	**0.57**	0.07	27.82	**10.53**	1.96	41.54	**1.58**	0.35	50.06	**1.33**	0.17	29.07
2	*Ponderosa pine*	**51.98**	0.21	0.90	**0.64**	0.07	24.24	**0.91**	0.11	26.99	**3.88**	0.40	23.03	**3.91**	0.72	41.02	**1.83**	0.12	14.08
2	*Western red cedar*	**52.56**	0.30	1.27	**0.46**	0.03	13.67	**0.56**	0.03	13.69	**23.45**	1.71	16.31	**3.27**	0.60	40.86	**1.05**	0.09	18.55
3	*big leaf maple*	**47.42**	0.42	1.96	**0.81**	0.10	26.32	**2.18**	0.14	13.98	**18.48**	1.61	19.49	**6.26**	0.41	14.78	**2.49**	0.63	56.83
3	*golden chinkapin*	**52.22**	0.22	0.92	**0.47**	0.08	35.57	**0.43**	0.03	15.99	**6.98**	0.77	24.59	**1.77**	0.20	25.40	**1.32**	0.13	21.71
3	*Oregon white oak*	**48.14**	0.32	1.51	**1.49**	0.12	18.34	**2.06**	0.23	24.45	**15.91**	1.28	18.02	**3.75**	0.27	16.39	**1.96**	0.08	9.30
3	*Pacific madrone*	**50.50**	0.33	1.46	**0.49**	0.16	70.63	**1.00**	0.09	21.06	**10.87**	1.80	37.11	**3.53**	0.81	51.29	**2.56**	0.39	33.95
3	*poplar*	**46.64**	0.62	2.98	**0.80**	0.18	48.91	**2.03**	0.30	33.01	**18.56**	2.60	31.36	**8.57**	0.77	19.99	**1.99**	0.26	29.34
3	*rhododendron*	**51.34**	0.40	1.73	**0.33**	0.02	12.09	**0.56**	0.06	23.46	**12.35**	0.81	14.75	**5.60**	0.43	16.99	**2.51**	0.22	19.30
3	*salal*	**49.74**	0.30	1.36	**0.44**	0.02	8.14	**0.41**	0.03	13.69	**16.11**	0.59	8.20	**3.40**	0.31	20.16	**3.87**	0.20	11.34
4	*Pacific dogwood*	**45.26**	0.21	1.03	**0.69**	0.04	13.96	**5.03**	0.31	13.82	**26.13**	1.89	16.20	**6.75**	0.65	21.39	**3.66**	0.12	7.35
4	*vine maple*	**44.76**	0.73	3.66	**0.94**	0.11	25.42	**2.91**	0.65	49.62	**15.45**	1.50	21.70	**7.57**	1.44	42.47	**5.53**	0.50	20.28
LSD		0.99			0.26			0.61			3.98			1.7			0.78		

Grouping of trees by common characteristics 1= nitrogen fixers; 2= conifers; 3= hardwoods and shrubs; 4= rapid decomposers
LSD= Least significant difference for mean separations, df= (16, 64), and alpha= 0.05.

Table 4. Expanded proximate analysis of leaf litter chemistry for each species (n= 5).

Group	Species	% Ash			% Non-polar Ext.			% Polar Extractives			% Total Extractives			% Acid Solubles		
		mean	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV
1	*red alder*	**4.54**	0.33	16.14	**5.02**	0.29	12.69	**39.47**	1.05	5.97	**44.49**	1.13	5.67	**36.23**	0.74	4.58
1	*Sitka alder*	**4.28**	0.18	9.15	**5.49**	0.33	13.41	**28.95**	0.50	3.84	**34.44**	0.64	4.13	**40.77**	0.86	4.71
1	*snowbrush*	**3.36**	0.43	28.90	**7.04**	0.10	3.28	**44.79**	1.37	6.86	**51.83**	1.35	5.84	**31.26**	0.48	3.42
2	*Douglas-fir*	**6.43**	0.14	4.94	**10.99**	0.31	6.34	**14.87**	1.23	18.53	**25.87**	1.27	10.97	**39.94**	0.57	3.19
2	*Pacific silver fir*	**3.94**	0.35	19.69	**10.40**	0.83	17.87	**37.61**	0.89	5.28	**48.01**	1.13	5.28	**30.02**	0.68	5.10
2	*ponderosa pine*	**3.52**	0.38	23.92	**8.87**	0.27	6.93	**22.13**	0.80	8.09	**31.00**	0.88	6.35	**40.30**	0.74	4.08
2	*western redcedar*	**6.41**	0.53	18.48	**10.80**	0.68	14.11	**26.26**	0.66	5.64	**37.06**	0.89	5.39	**36.47**	0.84	5.12
3	*bigleaf maple*	**9.62**	0.47	10.82	**8.86**	0.54	13.53	**19.81**	1.72	19.37	**28.67**	1.61	12.56	**45.93**	0.96	4.70
3	*golden chinkapin*	**2.57**	0.39	34.25	**5.64**	0.36	14.21	**31.08**	1.25	9.01	**36.72**	1.27	7.74	**41.99**	0.99	5.25
3	*Oregon white oak*	**6.72**	0.44	14.79	**4.33**	0.14	7.25	**24.09**	0.80	7.41	**28.42**	0.87	6.83	**42.77**	0.39	2.02
3	*Pacific madrone*	**4.32**	0.35	17.92	**4.56**	0.41	20.29	**39.59**	2.46	13.90	**44.16**	2.73	13.82	**35.39**	0.83	5.24
3	*poplar*	**9.36**	0.82	19.70	**6.49**	0.26	9.12	**32.58**	1.87	12.86	**39.07**	1.94	11.12	**39.11**	1.16	6.65
3	*rhododendron*	**4.39**	0.14	7.38	**5.50**	0.57	23.33	**32.45**	2.29	15.78	**37.95**	2.77	16.31	**40.76**	1.75	9.61
3	*salal*	**6.24**	0.20	7.23	**5.43**	0.26	10.71	**29.07**	1.18	9.10	**34.50**	1.40	9.04	**43.70**	0.56	2.88
4	*Pacific dogwood*	**10.98**	0.33	6.69	**6.19**	0.16	5.90	**48.53**	0.94	4.34	**54.72**	1.03	4.21	**39.06**	0.95	5.45
4	*vine maple*	**10.20**	0.79	17.28	**7.27**	0.86	26.37	**36.75**	1.36	8.29	**44.02**	1.91	9.72	**41.91**	1.92	10.27
LSD		1.23			1.30			3.90			4.38			2.79		

Grouping of trees by common characteristics 1= nitrogen fixers; 2= conifers; 3= hardwoods and shrubs; 4= rapid decomposers
Total Extractives is the polar extractives + the non-polar extractives.
LSD= Least significant difference for mean separations, df= (16, 64), and alpha= 0.05.

Table 4. Continued

Group	Species	%Klason Lignin			% Acid Soluble Lignin			% Total Lignin		
		mean	SE	CV	**mean**	SE	CV	**mean**	SE	CV
1	*red alder*	**19.27**	0.66	7.61	**5.75**	0.22	8.52	**25.03**	0.61	5.43
1	*Sitka alder*	**24.79**	0.51	4.56	**5.86**	0.26	10.03	**30.65**	0.50	3.66
1	*snowbrush*	**16.91**	1.31	17.31	**3.89**	0.10	5.73	**20.80**	1.36	14.59
2	*Douglas-fir*	**34.19**	1.22	7.98	**0.76**	0.07	20.17	**34.96**	1.24	7.92
2	*Pacific silver fir*	**21.97**	0.79	8.03	**1.81**	0.05	6.34	**23.78**	0.77	7.24
2	*ponderosa pine*	**28.70**	0.46	3.57	**1.17**	0.07	12.49	**29.87**	0.47	3.49
2	*western redcedar*	**26.47**	0.76	6.44	**1.57**	0.04	6.38	**28.04**	0.73	5.83
3	*bigleaf maple*	**25.40**	1.16	10.19	**2.07**	0.12	12.68	**27.47**	1.13	9.17
3	*golden chinkapin*	**21.30**	0.53	5.60	**2.29**	0.06	6.27	**23.59**	0.58	5.47
3	*Oregon white oak*	**28.81**	0.82	6.35	**2.01**	0.11	12.01	**30.82**	0.78	5.65
3	*Pacific madrone*	**20.46**	2.46	26.84	**4.19**	0.18	9.46	**24.65**	2.63	23.85
3	*poplar*	**21.82**	1.36	13.90	**1.69**	0.32	41.99	**23.52**	1.37	13.03
3	*rhododendron*	**21.29**	1.14	11.96	**2.21**	0.21	20.88	**23.50**	0.96	9.10
3	*salal*	**21.79**	0.98	10.02	**1.18**	0.02	4.71	**22.97**	0.98	9.56
4	*Pacific dogwood*	**6.22**	0.47	16.73	**6.54**	0.52	17.84	**12.76**	0.74	12.93
4	*vine maple*	**14.07**	0.17	2.71	**3.35**	0.18	11.99	**17.41**	0.19	2.38
LSD		2.99			0.57			3.06		

Grouping of trees by common characteristics 1= nitrogen fixers; 2= conifers; 3= hardwoods and shrubs; 4= rapid decomposers
Klason Lignin is defined as acid insoluble residue.
Total lignin is acid insoluble residue + acid soluble lignin.
LSD= Least significant difference for mean separations, df= (16, 64), and alpha= 0.05.

Table 5. Colormetric analysis of leaf litter chemistry for each species (n= 5).

Group	Species	Carbohydrates (mg glucose eq. g^{-1})									Polyphenolics (mg catechol eq. g^{-1})					
		Water Soluble			Acid Soluble			Total			Reactive			Total		
		mean	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV
1	*red alder*	**148.64**	9.76	14.68	**363.40**	24.83	15.28	**512.04**	21.81	9.53	**63.64**	3.45	12.13	**87.22**	3.50	8.98
1	*Sitka alder*	**82.89**	8.97	24.19	**451.66**	6.47	3.20	**534.55**	10.10	4.23	**36.92**	1.38	8.34	**48.94**	1.78	8.13
1	*snowbrush*	**145.43**	12.72	19.55	**319.76**	5.21	3.64	**465.19**	16.57	7.97	**68.82**	3.14	10.22	**87.44**	3.36	8.59
2	*Douglas-fir*	**68.17**	3.72	12.21	**413.69**	10.44	5.64	**481.86**	10.53	4.89	**10.55**	1.20	25.36	**20.37**	1.77	19.39
2	*Pacific silver fir*	**172.25**	15.56	20.20	**356.22**	13.09	8.22	**528.47**	18.11	7.66	**42.08**	3.89	20.68	**56.75**	3.36	13.24
2	*ponderosa pine*	**101.57**	2.89	6.36	**605.23**	9.11	3.37	**706.80**	9.38	2.97	**12.26**	2.64	48.12	**25.24**	2.89	25.60
2	*western redcedar*	**86.85**	5.83	15.02	**420.38**	12.43	6.61	**507.24**	9.59	4.23	**30.06**	2.36	17.53	**42.39**	2.55	13.47
3	*bigleaf maple*	**77.53**	6.38	18.40	**457.63**	20.10	9.82	**535.16**	24.26	10.14	**12.14**	4.91	90.55	**23.10**	5.20	50.36
3	*golden chinkapin*	**79.69**	1.30	3.64	**444.61**	16.77	8.44	**524.30**	16.19	6.90	**54.56**	4.98	20.43	**69.34**	5.31	17.12
3	*Oregon white oak*	**63.41**	2.24	7.91	**416.71**	9.56	5.13	**480.13**	11.00	5.12	**34.96**	3.35	21.45	**44.86**	3.49	17.40
3	*Pacific madrone*	**92.72**	12.90	31.12	**365.85**	24.35	14.88	**458.58**	29.89	14.58	**57.90**	6.79	26.23	**80.32**	8.72	24.27
3	*poplar*	**133.13**	16.82	28.25	**429.13**	15.44	8.04	**562.27**	24.73	9.84	**32.11**	5.15	35.85	**45.81**	4.79	23.37
3	*rhododendron*	**79.02**	1.33	3.76	**441.47**	16.15	8.18	**520.49**	15.50	6.66	**35.34**	4.65	29.41	**53.99**	6.07	25.14
3	*salal*	**92.77**	12.83	30.93	**366.79**	22.99	14.01	**459.56**	28.91	14.07	**34.95**	2.81	18.00	**46.11**	3.08	14.92
4	*Pacific dogwood*	**107.75**	9.03	18.74	**594.08**	11.05	4.16	**701.83**	17.64	5.62	**69.69**	4.22	13.53	**96.44**	4.60	10.66
4	*vine maple*	**87.25**	1.20	3.06	**608.68**	23.47	8.62	**695.93**	22.42	7.20	**44.29**	7.46	37.66	**61.19**	8.36	30.55
LSD		26.56			46.17			53.97			12.00			13.40		

Grouping of trees by common characteristics 1= nitrogen fixers; 2= conifers; 3= hardwoods and shrubs; 4= rapid decomposers
LSD= Least significant difference for mean separations, df= (16, 64), and alpha= 0.05.

Table 5. Continued

Group	Species	% Condensed Tannins														
		Water Soluble			Water Insoluble			Acid Insoluble			Total Insoluble			Total		
		mean	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV
1	*red alder*	**0.24**	0.02	17.65	**5.20**	0.20	8.71	**4.16**	0.09	4.85	**9.36**	0.26	6.24	**9.60**	0.25	5.78
1	*Sitka alder*	**0.26**	0.02	21.03	**11.98**	0.58	10.89	**12.15**	0.63	11.65	**24.13**	0.94	8.74	**24.39**	0.96	8.77
1	*snowbrush*	**1.12**	0.06	11.05	**22.92**	0.92	8.96	**6.87**	0.34	10.97	**29.79**	0.94	7.07	**30.90**	0.98	7.06
2	*Douglas-fir*	**0.45**	0.05	24.15	**9.11**	0.78	19.04	**3.05**	0.20	14.52	**12.16**	0.96	17.66	**12.61**	0.99	17.63
2	*Pacific silver fir*	**1.57**	0.14	20.30	**11.63**	1.70	32.63	**2.99**	0.19	14.55	**14.62**	1.85	28.30	**16.19**	1.89	26.13
2	*ponderosa pine*	**0.54**	0.11	44.98	**8.50**	0.84	22.08	**3.72**	0.21	12.76	**12.22**	0.95	17.34	**12.76**	1.03	17.97
2	*western redcedar*	**1.05**	0.07	15.61	**7.70**	0.23	6.80	**3.46**	0.14	9.29	**11.16**	0.35	7.04	**12.20**	0.37	6.78
3	*bigleaf maple*	**0.47**	0.07	35.23	**8.28**	1.53	41.22	**4.01**	0.46	25.60	**12.29**	1.95	35.53	**12.76**	2.02	35.35
3	*golden chinkapin*	**0.79**	0.06	16.09	**7.49**	0.46	13.64	**5.96**	0.25	9.19	**13.45**	0.69	11.51	**14.24**	0.68	10.72
3	*Oregon white oak*	**0.31**	0.05	32.68	**3.88**	0.35	20.12	**1.59**	0.02	2.49	**5.47**	0.35	14.46	**5.78**	0.40	15.36
3	*Pacific madrone*	**0.70**	0.08	24.71	**8.50**	0.94	24.81	**6.55**	0.65	22.14	**15.05**	1.58	23.45	**15.75**	1.56	22.22
3	*poplar*	**1.15**	0.22	42.34	**13.00**	1.70	29.25	**0.36**	0.03	17.94	**13.36**	1.73	28.94	**14.51**	1.62	24.94
3	*rhododendron*	**1.14**	0.10	19.01	**18.37**	0.93	11.36	**12.10**	0.67	12.30	**30.48**	1.38	10.16	**31.62**	1.40	9.93
3	*salal*	**1.70**	0.12	15.57	**12.80**	1.27	22.22	**7.87**	0.20	5.57	**20.67**	1.26	13.62	**22.38**	1.34	13.43
4	*Pacific dogwood*	**0.12**	0.01	15.27	**2.53**	0.09	8.02	**24.07**	1.55	14.43	**26.59**	1.62	13.63	**26.72**	1.62	13.58
4	*vine maple*	**0.21**	0.04	40.44	**4.70**	1.00	47.54	**15.44**	1.02	14.79	**20.14**	1.93	21.48	**20.35**	1.97	21.63
LSD		0.26			2.77			1.63			3.67			3.72		

Grouping of trees by common characteristics 1= nitrogen fixers; 2= conifers; 3= hardwoods and shrubs; 4= rapid decomposers
Condensed Tannins are calculated using the extinction coeffecient of 150 (Bate-Smith, 1973).
LSD= Least significant difference for mean separations, df= (16, 64), and alpha= 0.05.

Table 6. Predictive indicies of leaf litter quality for each species (n= 5).

Group	Species	C:N			C:P			N:P			RPP:N			PP :N			PP:P		
		mean	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV
1	*red alder*	**23.79**	1.17	10.98	**474.52**	45.12	21.26	**20.06**	1.81	20.21	**3.06**	0.29	20.94	**4.18**	0.34	18.42	**83.18**	9.87	26.55
1	*Sitka alder*	**20.47**	0.48	5.25	**279.75**	20.71	16.55	**13.77**	1.27	20.68	**1.52**	0.07	11.04	**2.01**	0.10	10.76	**27.29**	1.77	14.50
1	*snowbrush*	**38.47**	2.44	14.18	**682.15**	55.28	18.12	**17.65**	0.48	6.12	**5.04**	0.53	23.47	**6.40**	0.64	22.25	**113.65**	12.92	25.41
2	*Douglas-fir*	**98.88**	3.06	6.93	**740.70**	30.06	9.07	**7.53**	0.46	13.52	**2.02**	0.23	25.95	**3.90**	0.35	20.34	**28.84**	1.49	11.58
2	*Pacific silver fir*	**142.84**	9.55	14.95	**967.13**	118.21	27.33	**7.11**	1.30	41.01	**11.70**	1.59	30.30	**15.74**	1.74	24.69	**104.26**	11.87	25.45
2	*ponderosa pine*	**84.73**	8.83	23.29	**608.38**	77.42	28.45	**7.15**	0.34	10.73	**2.14**	0.61	63.49	**4.27**	0.87	45.35	**30.97**	6.86	49.57
2	*western redcedar*	**116.49**	7.10	13.63	**947.79**	57.95	13.67	**8.14**	0.13	3.64	**6.68**	0.69	22.98	**9.42**	0.87	20.72	**76.91**	7.62	22.14
3	*bigleaf maple*	**61.50**	6.04	21.94	**220.90**	14.76	14.94	**3.81**	0.60	34.94	**1.75**	0.88	113.18	**3.17**	1.04	73.08	**10.35**	1.94	41.91
3	*golden chinkapin*	**119.51**	15.20	28.44	**1234.54**	97.93	17.74	**10.96**	1.47	30.04	**12.95**	2.48	42.85	**16.39**	2.99	40.81	**165.82**	21.29	28.71
3	*Oregon white oak*	**33.14**	2.59	17.50	**243.43**	23.15	21.26	**7.52**	0.86	25.66	**2.47**	0.40	35.96	**3.15**	0.45	32.25	**22.85**	3.33	32.55
3	*Pacific madrone*	**141.22**	31.94	50.57	**523.94**	50.95	21.74	**5.06**	1.65	73.09	**17.82**	5.02	62.94	**24.53**	6.87	62.58	**84.01**	14.62	38.90
3	*poplar*	**70.89**	15.23	48.03	**253.33**	40.38	35.65	**4.54**	1.44	70.77	**5.35**	1.86	78.01	**7.32**	2.19	67.01	**23.98**	3.03	28.27
3	*rhododendron*	**155.88**	10.03	14.39	**956.83**	108.43	25.34	**6.07**	0.33	11.98	**10.92**	1.87	38.25	**16.64**	2.57	34.47	**103.31**	19.78	42.82
3	*salal*	**114.09**	3.60	7.06	**1231.28**	88.25	16.03	**10.83**	0.79	16.36	**7.98**	0.58	16.24	**10.54**	0.65	13.76	**112.90**	6.47	12.82
4	*Pacific dogwood*	**66.09**	3.53	11.93	**91.37**	5.62	13.74	**1.42**	0.16	25.85	**10.22**	0.96	21.05	**14.13**	1.18	18.62	**19.32**	0.90	10.39
4	*vine maple*	**49.83**	5.21	23.39	**197.43**	52.55	59.52	**3.85**	0.79	45.91	**5.09**	1.14	49.93	**6.99**	1.37	43.74	**28.57**	9.57	74.87
LSD		30.92			182.36			2.88			4.77			6.22			29.39		

Grouping of trees by common characteristics. 1= nitrogen fixers; 2= conifers; 3= hardwoods and shrubs; 4= rapid decomposers
RPP= Reactive polyphenolics
PP= Total Polyphenolics
LSD= Least significant difference for mean separations, df= (16, 64), and alpha= 0.05.

Table 6. Continued

Group	Species	Lignin:P			Lignin: N			(Lignin + PP)/ N)			Lignocellulose			Lignin: WS Carb.			PP: WS Carb.		
		mean	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV	**mean**	SE	CV
1	*red alder*	**182.85**	17.97	21.98	**9.15**	0.45	11.12	**13.33**	0.76	12.71	**0.35**	0.02	12.05	**1.33**	0.14	23.22	**0.60**	0.06	20.53
1	*Sitka alder*	**138.74**	9.58	15.45	**10.18**	0.37	8.02	**12.19**	0.42	7.77	**0.35**	0.01	3.83	**3.16**	0.41	29.22	**0.61**	0.05	18.85
1	*snowbrush*	**212.72**	9.82	10.32	**12.03**	0.32	5.95	**18.43**	0.56	6.75	**0.34**	0.02	13.55	**1.21**	0.16	28.85	**0.62**	0.04	16.17
2	*Douglas-fir*	**493.27**	36.96	16.75	**65.34**	2.10	7.20	**69.24**	1.87	6.04	**0.45**	0.01	5.85	**5.11**	0.44	19.37	**0.30**	0.01	7.71
2	*Pacific silver fir*	**412.67**	59.69	32.35	**60.12**	3.28	12.21	**75.86**	5.01	14.77	**0.38**	0.02	9.06	**1.32**	0.14	23.40	**0.35**	0.05	29.92
2	*ponderosa pine*	**334.78**	40.68	27.17	**46.61**	4.51	21.62	**50.88**	5.31	23.34	**0.32**	0.01	3.73	**2.84**	0.10	7.78	**0.25**	0.03	24.60
2	*western redcedar*	**475.44**	23.81	11.20	**58.45**	3.02	11.54	**67.88**	3.63	11.96	**0.39**	0.01	5.22	**3.10**	0.24	17.12	**0.50**	0.04	18.99
3	*bigleaf maple*	**118.79**	10.76	20.25	**32.66**	2.75	18.83	**35.83**	3.26	20.35	**0.36**	0.02	11.37	**3.37**	0.34	22.41	**0.30**	0.07	48.76
3	*golden chinkapin*	**503.02**	39.93	17.75	**48.22**	5.31	24.63	**64.60**	8.27	28.63	**0.32**	0.01	5.41	**2.68**	0.10	8.25	**0.87**	0.07	17.57
3	*Oregon white oak*	**145.79**	14.06	21.56	**19.68**	1.10	12.53	**22.83**	1.55	15.22	**0.41**	0.01	6.30	**4.58**	0.29	14.03	**0.71**	0.05	16.57
3	*Pacific madrone*	**209.51**	26.36	28.13	**51.30**	8.14	35.50	**75.83**	14.69	43.31	**0.36**	0.04	26.74	**2.40**	0.45	42.03	**0.93**	0.15	34.98
3	*poplar*	**121.02**	24.08	44.50	**33.01**	6.81	46.11	**40.33**	8.75	48.50	**0.34**	0.02	12.43	**1.78**	0.30	38.00	**0.36**	0.04	26.93
3	*rhododendron*	**392.77**	41.95	23.88	**64.30**	4.26	14.83	**80.94**	5.29	14.61	**0.33**	0.02	11.16	**2.70**	0.17	14.05	**0.68**	0.07	23.13
3	*salal*	**545.18**	63.00	25.84	**49.90**	2.35	10.51	**60.44**	1.99	7.35	**0.37**	0.02	14.54	**2.52**	0.33	29.42	**0.55**	0.09	37.34
4	*Pacific dogwood*	**12.68**	1.54	27.24	**8.94**	0.17	4.33	**23.08**	1.17	11.34	**0.09**	0.01	17.52	**0.60**	0.09	32.77	**0.92**	0.08	18.47
4	*vine maple*	**61.72**	16.24	58.82	**15.62**	1.56	22.35	**22.61**	2.78	27.47	**0.19**	0.01	6.78	**1.61**	0.03	4.75	**0.70**	0.09	28.46
LSD		91.65			10.50			15.57			0.05			0.76			0.19		

Grouping of trees by common characteristics 1= nitrogen fixers; 2= conifers; 3= hardwoods and shrubs; 4= rapid decomposers
PP= Total Polyphenolics
WS Carb. = Water soluble carbohydrates
Klason Lignin= Acid Insoluble Residue
(Klason Lignin + PP)/ N= Fox et al. (1990) index
Lignocellulose= "Klason Lignin"/ ("Klason Lignin" + Acid Soluble Carbohydrates)
LSD= Least significant difference for mean separations, df= (16, 64), and alpha= 0.05.

The elemental analysis showed (Table 3) that within each physiological group, individual species have similar chemical qualities. The species were relatively similar in their carbon content, vine maple had the lowest % C with 44.8% and snowbrush had the highest % C with 53%. The average % nitrogen however had a wide range between species, from 0.33% for Pacific rhododendron to 2.44% for Sitka alder (a nitrogen fixing species). In general all three nitrogen fixers had percentages of N over 1% and were greater than all the other species except for Oregon white oak with 1.5% N. The range of phosphorus content was smaller across all species, with salal having 0.41 mg/g P on the low end and dogwood having 5.0 mg/g P on the high end and there was little difference by physiological group. Calcium content ranged from 3.9 mg/g for ponderosa pine to 26.1 mg/g for dogwood, the potassium content ranged from 0.56 mg/g for Douglas-fir to 8.6 mg/g for poplar, and the magnesium content ranged from 0.9 mg/g for Douglas-fir to 5.5 mg/g for vine maple.

The expanded proximate analysis (Table 4) also showed distinctive patterns between species groups. Dogwood and vine maple had the highest % ash, with 11.0 and 10.2% respectively, following the results of the elemental analysis. Golden chinkapin had the lowest ash content with only 2.6%. The % non-polar extractive fractions were similar between species except for the conifers which had over 10%. The polar extractive fraction did not have a strong species grouping pattern and ranged from 20% for bigleaf maple to

48.5% for dogwood. The total extractive fraction was calculated by the addition of the non-polar and the polar extractives. The values for this variable ranged from 25.9% for Douglas-fir to 54.7% for dogwood. The acid-soluble fraction was also similar between species groups and ranged from 30% for Pacific silver fir to 45.9% for bigleaf maple. Klason lignin however, did have a species grouping pattern especially for the conifers and the rapid decomposers. The range was from 6.2% for dogwood to 34.2% for Douglas-fir. This pattern also held for the acid-soluble lignin fraction, which ranged from 0.8% for Douglas-fir to 6.5% for dogwood. Finally, the total lignin fraction (calculated as lignin plus the acid-soluble fraction) followed this same pattern with 12.8% for dogwood and 35% for Douglas-fir.

The colorimetric analysis (Table 5) also displayed species grouping patterns for some of the chemical variables. For the water-soluble carbohydrate fraction the range was from 63.4 mg glucose eq./g sample for Oregon white oak to 172.3 mg/g for Pacific silver fir. The acid-soluble carbohydrate fraction ranged from 320 mg/g for snowbrush to 608 mg/g for vine maple and the total carbohydrate fraction (water plus acid-soluble carbohydrates) ranged from 460 mg/g for rhododendron to 706 mg/g for ponderosa pine. The total phenolic fractions ranged from 20.4 mg catechol eq./g sample for Douglas-fir to 96.1 mg/g for dogwood and the reactive fraction was from 10.6 mg/g for Douglas-fir to 69.7 mg/g for dogwood following trends observed in the proximate analysis. Water-soluble condensed tannins ranged

from 0.12 % for dogwood to 1.7 % for salal, water-insoluble condensed tannins ranged from 2.5 % for dogwood to 22.9% for snowbrush, acid-insoluble condensed tannins ranged from 0.4% for poplar to 24.1% for dogwood, total tannins (water-soluble + water-insoluble + acid insoluble) ranged from 5.8% for Oregon white oak to 31.6% for rhododendron, and total insoluble condensed tannins (water-insoluble plus acid insoluble) ranged from 5.5% for Oregon white oak to 30.5 % for rhododendron.

The predictors generated as basic chemical ratios (Table 6) show some grouping patterns along physiological lines. The C:N range was from 20.5 for Sitka alder to 156 for rhododendron, the C:P range was from 91.4 for dogwood to 1234.5 for chinkapin, the N:P range was from 1.4 for dogwood to 20.1 for red alder, for the RPP:N the range was from 1.5 for Sitka alder to 17.8 for Pacific madrone, the total phenolics:N range was from 2.0 for Sitka alder to 24.5 for Pacific madrone, and the total phenolics:P range was from 10.4 for bigleaf maple to 165.8 for golden chinkapin. The rapid decomposers had the smallest lignin:P value; the numbers ranged from 12.7 for dogwood to 545.8 for salal. The lignin:N were lowest in the rapid decomposers and the nitrogen fixers and the highest in the conifers and hardwoods. The range was from 8.9 for dogwood to 65.3 for Douglas-fir. The Fox et al. (1990) index of Lignin+ total phenolics:N ranged for 12.2 for Sitka alder to 81.0 for rhododendron. The lignocellulose index of lignin/(lignin + acid-soluble carbohydrates) ranged from 0.09 for dogwood to 0.45 for Douglas-fir. The lignin: water-soluble

carbohydrates ranged from 0.6 for dogwood to 5.1 for Douglas-fir and the total phenolics:water-soluble carbohydrates ranged from 0.25 for ponderosa pine to 0.92 for Pacific madrone.

There was generally high intraspecific variability in chemical composition. The smallest CV of the 36 measurements of litter quality was with C (range from 0.32-3.66). The proximate fractions (non-polar extractives, polar extractives, total extractives, acid-solubles, "Klason lignin", acid-soluble lignin, and total lignin), carbohydrate fractions (water-soluble, acid-soluble and total), acid-soluble condensed tannins, lignocellulose, and C:P all had more consistent patterns of variability, i.e. in the range of approximately 5-30%. Where as, Ca, ash, condensed tannins (except for acid-insoluble condensed tannins), (Klason lignin +PP):N, Lignin:N, PP:water-soluble carbohydrates, and lignin:water-soluble carbohydrates all had much broader ranges, i.e. approximately 5-45%. On the extreme side was N, P, K, Mg, all the polyphenolic measurements, C:N, N:P, RPP:N, PP:N, PP:P, and Lignin:P had CV's from 5-110%, implying that there was greater variation within species in these measurements.

Initial Litter Quality Predictions of Decomposition

Thirty-six predictors (including previously used ratios from decomposition studies displayed in Table 1) were used to test how initial chemistry qualities predicted decomposition rates (k) of all 16 species together. The results of a simple linear correlation analysis between the k-values and each predictor are displayed in Table 7. Of the 36 predictors tested, 29 were highly significant (p <0.0001) in explaining the decay value. These results show that annual decomposition rate constants for all species combined were most strongly correlated (r) with acid-insoluble condensed tannins (r= 0.83), followed closely by "Klason lignin" (r= -0.80) and the lignocellulose index (r= -0.81). The first four variables each explain at least 50% of the variation in k-value and the next 12 variables explain at least 25% of the variation. The results also show that reactive polyphenolics are a mid range predictor (r= 0.54) of decomposition and are better than the % N (r= 0.19) or the C:N (r= -0.29).

Correlation analyses for individual species are displayed in Table 8, show that no one initial chemical variable was common to all species and that a wide range of variables can predict each species decomposition rates. There were four variables that were found to be significant (p < 0.01) in predicting decomposition for at least four species, i.e. polar extractives, reactive polyphenolics, acid-insoluble condensed tannins, and P.

Table 7. Ordered correlations (r) of the individual chemistry variables as predictors of decay (k) of all species combined (n=339).

Variable	Correlation (r)	*p*
1. Acid-insoluble Condensed Tannins	0.826	<0.0001
2. Lignocellulose index	-0.805	<0.0001
3. "Klason lignin" or Acid-insoluble Residue	-0.801	<0.0001
4. Total Lignin	-0.716	<0.0001
5. Acid-soluble Lignin	0.673	<0.0001
6. P	0.654	<0.0001
7. Polar Extractives	0.619	<0.0001
8. Lignin: N	-0.578	<0.0001
9. Total Phenolics	0.577	<0.0001
10. Lignin: Water-soluble Carbohydrates	-0.569	<0.0001
11. C	-0.565	<0.0001
12. Total Extractives	0.564	<0.0001
13. Mg	0.557	<0.0001
14. Reactive Polyphenolics	0.537	<0.0001
15. Lignin:P	-0.523	<0.0001
16. Total Insoluble Condensed Tannins	0.470	<0.0001
17. Total Carbohydrates	0.467	<0.0001
18. Acid-soluble Carbohydrates	0.459	<0.0001
19. (Lignin+ Total Phenolics) :N	0.452	<0.0001
20. Total Phenolics: Water-soluble Carbohydrates	0.442	<0.0001
21. Total Condensed Tannins	0.437	<0.0001
22. Water-soluble Condensed Tannins	-0.428	<0.0001
23. K	0.426	<0.0001
24. Ash	0.407	<0.0001
25. C:P	-0.388	<0.0001
26. Non Polar Extractives	-0.298	<0.0001
27. C:N	-0.292	<0.0001
28. Water-insoluble Condensed Tannins	-0.259	<0.0001
29. Ca	0.256	<0.0001
30. N	0.188	0.0005
31. N:P	-0.120	0.0274
32. Total Phenolics: P	-0.120	0.0276
33. Reactive Polyphenolics: N	0.090	0.0967
34. Water-soluble Carbohydrates	0.085	0.1202
35. Acid Solubles	0.079	0.1442
36. Total Phenolics: N	0.078	0.1522

To test the influence of the clustering associated with each physiological group (Figures 3-4), particularly for the rapid decomposers (group 4) and for the conifers (group 2), the analysis was expanded to examine the relationship between decay of each physiological group and the independent chemistry variables. These analyses included models without the rapid decomposers and models without the conifers (Table 8). These analyses showed that there was only one variable that predicted the decomposition rates of the nitrogen fixer group, where as the conifers, hardwoods and rapid decomposers had many variables correlated with their decay values. The lignocellulose index had the highest correlation with the decay of the nitrogen fixer group ($r= -0.34$), water-soluble carbohydrates had the highest correlation with the conifer group ($r= 0.69$), ash and total phenolic:P were each best correlated with the hardwood group ($r= -0.5$ and $r= 0.5$ respectively), and acid-soluble lignin was the highest correlate with the rapid decomposers ($r= 0.70$). Looking at all the data without the rapid decomposers suggested that acid-soluble lignin ($r= 0.56$) followed closely by Klason lignin ($r= -0.54$) had the highest overall correlations with the decay rate and looking at all the data without the conifers the highest correlation was with water-insoluble condensed tannins ($r= 0.8$).

Table 8. Correlations (r) of decay (k) and litter chemistry for individual species, physiological species groups and all species together ($p < 0.01$).

						Tot	Acid	Lignin			Carbohydrates			Phenolics		Cond. Tannins				
Group	Species	n	ash	NPE	PE	Ext.	Sol.	AI	AS	TOT	WS	AS	TOT	WS	RPP	WS	WI	AI	TOT	TOT I.
1	*red alder*	13																		
1	*Sitka alder*	24																		
1	*snowbrush*	25			0.50			-0.56		-0.56		0.65						0.63		
2	*Douglas-fir*	15			0.69	0.70		-0.62			0.67			0.65	0.64					
2	*Pacific silver fir*	25			0.64	0.68	-0.68				0.61		0.51		-0.52					
2	*ponderosa pine*	24			-0.63	-0.66	0.79					0.73	0.73	-0.60	-0.57	-0.55	-0.53	-0.73	-0.65	-0.64
2	*western redcedar*	23									0.54									
3	*bigleaf maple*	15							-0.75											
3	*golden chinkapin*	25																		
3	*Oregon white oak*	15												-0.61	-0.61					
3	*Pacific madrone*	24															-0.55	-0.64	-0.61	-0.59
3	*poplar*	14																		
3	*rhododendron*	25										0.48	0.50							
3	*salal*	23		0.52				-0.60	-0.53	-0.61							-0.59	0.61		
4	*Pacific dogwood*	24																		
4	*vine maple*	25																		
Nitrogen Fixers (1)		62																		
Conifers (2)		87	-0.48		0.55	0.51	-0.44	-0.53	0.37	-0.54	0.69			0.29		0.28	0.38	0.32	0.33	0.31
Hardwoods (3)		141	-0.50					-0.36		-0.37		0.24	0.24	0.27	0.26			0.38	0.24	0.23
Rapid Decom. (4)		49			0.62	0.47		-0.65	0.70	-0.53	0.42			0.49	0.44	-0.48	-0.41	0.66	0.53	0.54
Without Group 4		290	-0.41	-0.44	0.46	0.34		-0.54	0.56	-0.38	0.18			0.51	0.50		0.26	0.50	0.39	0.40
Without Conifers-group 2		252	0.40	0.19	0.57	0.59		-0.78	0.57	-0.67	0.17	0.66	0.73	0.47	0.43	-0.47	-0.37	0.80	0.31	0.35
All Species		**339**	**0.41**	**-0.30**	**0.62**	**0.56**		**-0.80**	**0.67**	**-0.72**		**0.47**	**0.47**	**0.58**	**0.54**	**-0.43**	**-0.26**	**0.83**	**0.44**	**0.47**

NPE= non-polar extractives PE= polar extractives
Lignin: AI= acid-insoluble or Klason Lignin; AS= acid-soluble; TOT= total
Carbohydrates: WS= water-solulbe, AS= acid-soluble, TOT= total
Phenolics: WS= total water-soluble phenolics; RPP= reactive polyphenolics.
Condensed Tannins: WS= water-soluble; WI= water-insoluble; AI= acid-insoluble; TOT I.= total insoluble.

Table 8. Continued

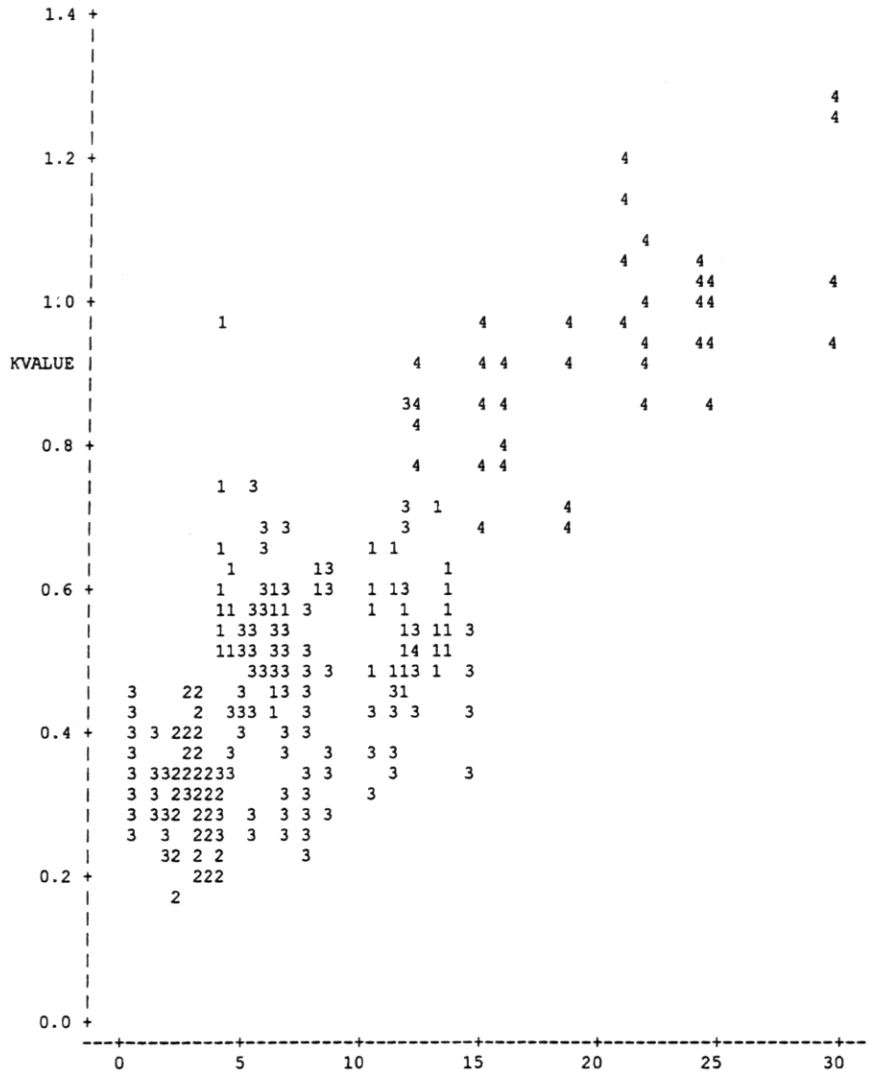
Group	Species	n	C	N	C:N	P	C:P	K	Ca	Mg	Lig: N	RPP: N	PP: N	(Lig+ PP): N	Lig- cell	Lig: carb	PP: carb	PP: P	Lig: P	N:P
1	*red alder*	13				-0.67	0.68											0.66	0.68	
1	*Sitka alder*	24																		
1	*snowbrush*	25									-0.63				-0.60					
2	*Douglas-fir*	15				0.69	-0.68	0.72		0.71	-0.65	0.64	0.64			-0.66			-0.66	
2	*Pacific silver fir*	25						0.70								-0.64	-0.56			
2	*ponderosa pine*	24				0.54								-0.68			-0.60			-0.68
2	*western redcedar*	23														-0.54	-0.62		-0.54	
3	*bigleaf maple*	15																		
3	*golden chinkapin*	25																		
3	*Oregon white oak*	15																		
3	*Pacific madrone*	24																		
3	*poplar*	14																		
3	*rhododendron*	25																		
3	*salal*	23								-0.58										
4	*Pacific dogwood*	24				-0.55	0.56					-0.56	-0.56	-0.58						0.54
4	*vine maple*	25										0.00								
Nitrogen Fixers (1)		62													-0.34					
Conifers (2)		87							-0.37	0.28		0.29	0.34			-0.62	-0.39		-0.45	-0.33
Hardwoods (3)		141	0.49	-0.37	0.36	-0.48	0.47	-0.25	-0.48		0.33	0.28	0.28	0.33	-0.37	-0.29		0.50	0.39	0.24
Rapid Decom. (4)		49		-0.37	0.38				0.44	-0.55	-0.57	-0.44	0.47		-0.62	-0.64			-0.41	-0.38
Without Group 4		290		0.41	-0.20			0.17	-0.33	0.16	-0.41			0.30	-0.38	-0.39	0.31	0.34	-0.19	0.53
Without Conifers-group 2		252	-0.45		-0.20	0.61	-0.32	-0.29	0.33	0.43	-0.45			-0.33	-0.81	-0.60	0.27	-0.20	-0.40	-0.19
All Species		**339**	**-0.57**	**0.19**	**-0.29**	**0.65**	**-0.39**	**0.43**	**0.26**	**0.56**	**-0.58**			**-0.45**	**-0.81**	**-0.57**	**0.44**		**-0.52**	

Lignin: acid-insoluble residue or Klason Lignin
Carb= water-soluble carbohydrates
PP= total water-soluble phenolics; RPP= reactive polyphenolics.
Ratios= lignin: N; reactive polyphenolics: N; total WS phenolics: N; (lignin + total WS phenolics):N; lignocellulose index; lignin: WS carbohydrates; total phenolics: WS carbohydrates; total phenolics:P; lignin:P; N:P.

Figure 3. Clustering by physiological groups of decay (k) versus acid-insoluble condensed tannins.

Equation: $\ln(y) = 0.26\ (0.01) + 0.03\ (0.001)\ x$

SE in parentheses
y= % weight remaining
x= acid-insoluble condensed tannins
SE in parentheses
R^2=0.68
n=339
p <0.0001

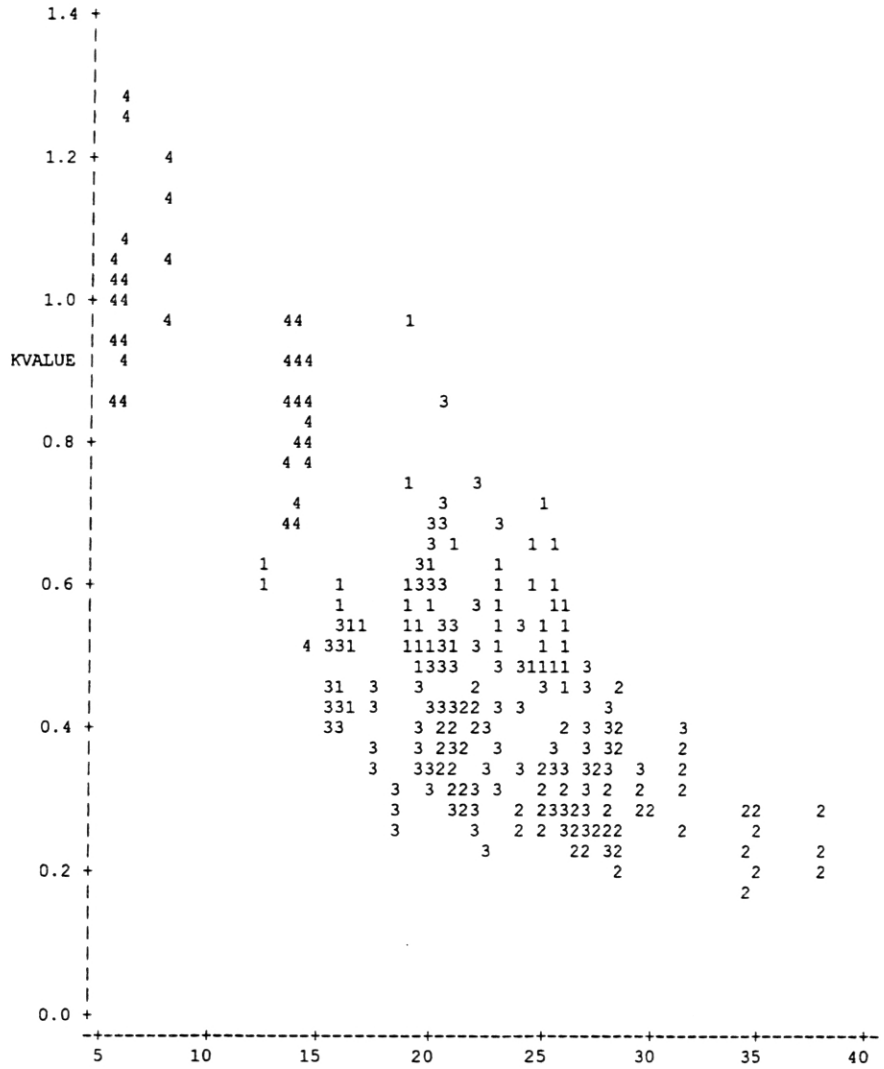


Trees were grouped by common characteristics.
1= nitrogen fixers; 2= conifers; 3= hardwoods and shrubs; 4 is for the rapid decomposers.

Figure 4. Clustering by physiological groups of decay (k) versus "Klason lignin".

Equation: $\ln(y) = 1.07\ (0.025) - 0.027\ (0.001)\ x$

SE in parentheses
y=% weight remaining
x ="Klason lignin"
SE in parenthesis
$R^2 = 0.64$
n = 339
$p < 0.0001$



NOTE: 11 obs had missing values. 128 obs hidden.

Trees were grouped by common characteristics.
1= nitrogen fixers; 2= conifers; 3= hardwoods and shrubs; 4 is for the rapid decomposers.

The multiple regression model to find the best **set** of litter quality variables for all species combined are summarized Table 9. This analysis shows that one year decomposition dynamics were most strongly related to acid-insoluble condensed tannins - "Klason lignin" - water-insoluble condensed tannins - Ca - total phenolics:N (R^2=0.84 p=0.0001 n=339). In this model acid-insoluble condensed tannins accounted for 68%, "Klason lignin" accounted for 9%, and water-insoluble condensed tannins, Ca and the total phenolics:N each accounted for 2% of the variation in the decay of all the species combined.

Table 9. ANOVA from the all species model with decay (k).

Source	DF	Sum of Squares	Mean Square	*F*	*P*
Model	5	14.00578	2.80116	373.029	0.0001
Error	333	2.50057	0.00751		
C Total	338	16.50636			

Root MSE	0.08666	R-square	0.8485
Dep Mean	-0.48973	Adj R-sq	0.8462
C.V.	-17.69465		

Parameter Estimates

Variable	DF	Mean	SE	t	*P*
Intercept	1	1.03	0.041	24.823	0.0001
Acid-insoluble cond. tannin	1	0.02	0.001	13.818	0.0001
Klason lignin	1	- 0.02	0.001	-17.590	0.0001
Water-insoluble cond. tannin	1	- 0.01	0.001	-8.276	0.0001
Ca	1	- 0.06	0.008	-7.729	0.0001
Total phenolics:N	1	- 0.06	0.008	-7.729	0.0001

Table 10. First, second, and third best predictors of decay values from step-wise multiple linear regression models for each individual species, physiological species groups and all species together ($p < 0.05$).

						Tot	Acid	Lignin			CHO			PHE		Cond. Tannins																				
Group	Species	n	ash	NPE	PE	Ext	Sol.	AI	AS	TOT	WS	AS	TO	WS	RPP	WS	WI	AI	TOT	TOT I.	C	N	C:N	P	C:P	K	Ca	Mg	Lig: N	RPP: N	PP: N	(Lig+ PP):N	Lig- cell	Lig: carb	PP: carb	PP: P	Lig: P	N:P	model R^2
1	*red alder*	13																																				0.46
1	*Sitka alder*	24										1																										none
1	*snowbrush*	25																								1												0.42
2	*Douglas-fir*	15																			2					1												0.52
2	*Pacific silver fir*	25					1										2																					0.57
2	*ponderosa pine*	24						2																														0.70
2	*western redcedar*	23							1			2																							1			0.46
3	*bigleaf maple*	15																																				0.72
3	*golden chinkapin*	25												1																								none
3	*Oregon white oak*	15																1									2											0.38
3	*Pacific madrone*	24				1																																0.75
3	*poplar*	14											1									3													2			0.37
3	*rhododendron*	25				2				1								3																				0.60
3	*salal*	23																														1						0.61
4	*Pacific dogwood*	24																																				0.34
4	*vine maple*	25																																				none
Nitrogen Fixers (1)		62															2																1					0.23
Conifers (2)		87									1										3		2															0.63
Hardwoods (3)		141	1																														2		3			0.47
Rapid Decom. (4)		49							1																													0.48
Without Group 4		290						2	1								4																					0.49
Without Conifers		252															2																1				3	0.80
All Species		339						2								3	1									4				5								0.84

NPE= non-polar extractives
PE= polar extractives
Lignin: AI= acid-insoluble or Klason Lignin; AS= acid-soluble; TOT= total
CHO= Carbohydrates; WS= water-solulbe, AS= acid-soluble, TOT= total
PHE= total water-soluble phenolics; RPP= reactive polyphenolics.
Condensed Tannins: WS= waters-soluble; WI= water-insoluble; AI= acid-insoluble; TOT I.= total insoluble.
Ratios= lignin: N; reactive polyphenolics: N; total WS phenolics: N; (lignin + total WS phenolics):N; lignocellulose index; lignin: WS carbohydrates; total phenolics: WS carbohydrates; total phenolics:P; lignin:P; N:P.

Multiple linear regression models run for each species and for groups of physiologically similar species (Table 10) also found no one set of predictors could explain decomposition for all groups. To test of the influence of the rapid decomposers, a model of decomposition without the rapid decomposers (Table 10) was examined. The results of this analysis suggest that the inclusion of these species (with low lignin values) does greatly influence the predictive models. This model found an association between acid-soluble lignin, Klason lignin, N:P and acid-insoluble condensed tannins with an overall lower correlation than the all species model (R^2= 0.49, p-value <0.0001, n= 290). To test the influence of the conifer group on the all-species model, a model without the conifers was examined. In this model acid-insoluble condensed tannins, lignocellulose index, acid-insoluble condensed tannins and N:P produced the best fit (R^2= 0.80, p-value <0.0001, n= 252).

Principle components analysis was used to check the results of the multiple regression analysis with all species included (Table 9). This analysis suggested that the first 6 eigenvectors accounted for 87% and the first 27 eigenvectors accounted for 99% of the variation in the 36 independent variables. Though the eigenvectors were not easily interpretable, the first component was a ratio of the lignin variables to the acid-insoluble condensed tannin, polar extractive and P variables which accounted for 35% of the variation. The second component was a contrast of the total phenolic:P, RPP:N and total phenolic:N variables to the acid solubles and the acid-soluble

carbohydrate fractions; it accounted for an additional 22% of the variation. A second data set was also tested that excluded the 12 variables that were ratios of the independent variables. The results of the two PCA analyses were very similar. This second analysis suggested that the first 6 eigenvectors accounted for 88% and the first 17 eigenvectors accounted for 99% of the variation in the independent variables. The first eigenvector was the same as in the first analysis where as the second component was a contrast of water-insoluble condensed tannins and carbon to the acid solubles and the acid-soluble carbohydrate fractions.

Discussion

Litter Quality Variability

There was generally a high degree of variability both between and within species for each chemical characteristic. This variability was often seen to cluster around the physiological groups (i.e. conifers, nitrogen fixers, hardwoods and shrubs and rapid decomposers). The variability is expected (Findlay 1996, Taylor and Parkinson 1988) because the broad physiological range of species studied and because the litter for each species was collected from five locations in western Oregon, which differed in elevation, aspect and microclimate. Overall, of the qualities measured, C was the most stable (i.e. lowest CV) of all the measurements, followed by the proximate and carbohydrate fractions, lignocellulose index, C:P and acid-soluble condensed tannins. Higher CV were seen in the polyphenolic measurements and the indices of decomposition suggesting that these fractions are more likely to be influenced by in situ climatic and soil characteristics.

Initial Litter Quality Predictions of Decomposition

When all plant species in this temperate forest environment were analyzed together, highly significant linear correlations (p <0.0001) were found between decay rates and litter characteristics for 29 out of the 36 predictors (Table 7). The first four predictors, acid-insoluble condensed tannins, lignocellulose index, Klason lignin, and total lignin each explained

approximately 50% of the variation in the decay rate. These predictors were likely to explain the decay the best because they include an assessment of the acid-insoluble residue and this residue has been shown by many to be very resistant to decomposition (see Table 1). The next twelve predictors, explained between 25-50% of the variation in the decay of all the species. These predictors included: 1) P and Mg which are essential nutrients; 2) some of the easily leached and higher carbon based nutrients (total phenolics, total carbohydrates, total extractives, and acid-soluble lignin) and ; 3) several of the common lignin based predictors of decomposition (i.e. Klason lignin:N, Klason lignin: P, Klason lignin: water-soluble carbohydrates). The remaining predictors explain less than 25% of the decay rate variation.

In contrast to the other studies (Table 1), neither N alone or C:N were effective predictors of decay rates. The lack of correlation between decay rates and total C: total N can be explained by the wide range of forms and decomposability of these elements in plant material. Cotrufo et al. (1995) have also shown the limitation of C:N as a predictor. In their study, birch litter was grown to have widely varying C:N ratios. Initially they found that the litters had different decay slopes, but after one year of decomposition, the litters had the same weight. Although N did not prove to be an effective predictor in our study, N could become more important in the later phases of decomposition when N becomes complexed with phenolics in a way that removes N from the pool of biologically available N.

In other studies (Table 1), lignin:N and total phenolics:N have been found to be good predictors of decomposition. In our study, Klason lignin:N was one of the better predictors (r= -0.58) but total phenolics:N was not. The poor performance of the total phenolics:N and the stronger performance of Klason lignin:N suggests that lignin is likely to be very influential in temperate forests. This finding is supported by the tropical research of Palm and Sanchez (1991) who found that the total phenolic:N was a better predictor of N mineralization than lignin:N. Furthermore, in our study there was relatively little difference between Klason lignin:N (r= -0.58) and Klason lignin:P (r= -0.52) in predicting decomposition, which further supports the role of lignin in temperate forest ecosystems.

In comparison with the information summarized in Table 1, the results of our study are not driven by significantly different ranges in leaf litter N or lignin content. With the exception of the higher N values reported by Palm and Sanchez (1991) for tropical trees, Peevy and Norman (1948) and Tian et al. (1992), the range of N concentrations found in our study were within the range reported by others (Table 1). Even though different techniques were used to measure lignin fractions in the studies listed in Table 1, the values observed in this study were also within the range reported (Table 1). The exceptions were the higher lignin concentrations reported by Fogel and Cromack (1977), Tian et al. (1992), and Hobbie (1996).[1] Despite the fact that N and lignin

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[1] For a comparison of lignin analytical techniques see Johansson et al. 1986, Ryan et al. 1990 and Heal 1997.

concentrations were within the same range reported by others, we would not expect to find the same relationships between N or lignin and decay because of confounding factors controlling litter decay. These factors include differences in climatic conditions, decomposer communities, soil nutrient availabilities, and soil and ecosystem types (temperate, tropical, boreal, or grasslands).

The predictors tested in this study had both negative and positive correlations with decay. A negative correlation implies that higher levels or concentrations of a predictor were associated with lower rates of decay. Higher concentrations of lignin and higher levels of the lignocellulose index were associated with lower decay (i.e. retarding decay) in the all-species model. These patterns have also been reported by Flanagan and Van Cleve (1983), Fogel and Cromack (1977), Mentenmeyer (1978), Gallardo and Merino (1993) and Mellilo et al. (1989). Negative correlations in our study were also found with water-soluble condensed tannins (r= -0.43), NPE (r= -0.30), lignin:N (r= -0.58), lignin:water-soluble carbohydrates (r= -0.57) and lignin:P (r= -0.52). Of these, the relationship between Lignin:P and decomposition has also been reported by Gallardo and Merino (1993). These finding suggest at least three factors controlling litter decomposition rates: 1) lignin decomposes very slowly so the greater the concentration of lignin the slower the decomposition rates; 2) leaf waxes (measured as NPE's) may also act as barriers to microbial decomposers; 3) water-soluble condensed tannins can inhibit decomposition (Swift et al. 1979 and Cadisch and Giller 1997).

There were several variables found to be positively correlated with the decay in the all-species model (i.e. higher concentrations were associated with higher levels of decay). These included acid-insoluble condensed tannins (r= 0.83), acid-soluble lignin (r= 0.67), P (r= 0.65), water-soluble total phenolics (r= 0.58), RPP (r= 0.54), Mg (r= 0.56), K (r= 0.43), Ca (r= 0.26), and N (r= 0.19). The positive correlation with water-soluble total phenolics, does not follow the findings of Tian et al. (1992), Findlay et al. (1996), Vallis and Jones (1973) or Gallardo and Merino (1993), who showed that higher concentrations of total phenolics retarded decomposition. In this study the water-soluble phenolics may have accelerated decay because they were quickly leached or used as a carbon source. It stands to reason that a more soluble form of lignin (acid-soluble lignin), and the essential nutrients (P, K, Mg, K, and N) all were associated with higher levels of decomposition. The high correlation with P and the low correlation with N, suggests that this forest had abundant N and concentrations of P may be limiting. P has been found to be important in predicting decomposition rates in several studies (Schlesinger and Hasey 1981, Staaf and Berg 1982, Aerts and de Caluwe 1997). Mg and K may also have a role with decay because they are essential nutrients.

The positive correlation with acid-insoluble condensed tannins and decay in the all-species model is not easy to interpret. It implies that higher concentrations of acid-insoluble condensed tannins were associated with higher rates of decay. This tannin fraction is typically included in the

measurement of Klason lignin during proximate analysis and is likely to be attached to the other acid-insoluble components, e.g. lignin and cutin. Perhaps the condensed tannin assay on the acid-soluble residue measures individual flavanoids that are linked into cutin and lignin which do react with BuOH-HCl but lack the degree of polymerization to complex with cytoplasmic proteins (Spencer et al. 1988). An alternative explanation is that as the lignin within the cell is degraded, the inhibitory effects of the tannins on decomposition become enhanced and only a longer study would show tannins inhibiting decay. Our finding is also contrary to the results of Mesquita et al. 1998 who showed that in the tropics, litter with higher condensed tannins concentrations in the neutral-detergent fiber residue (another measurement of lignin) were associated with slower decomposition at 1.5 years. Perhaps if these acid-insoluble condensed tannins retain their reactive ability to bind protein in later stages of decay, their presence may be a way to sequester nutrients and provide a mechanism to explain how N or P concentrations increase in the litter over time (Edwards 1980, Schlesinger and Hasley 1981, Maheswaran and Attiwill 1987, Mellilo et al. 1989, Tian et al. 1992)?

The positive correlation with RPP's in the all-species model was a surprise. We hypothesized that this measurement would confirm the complexing ability of many phenolics with N and P compounds and show that greater concentrations were associated with a reduction in decomposition rates. Contrary to our hypothesis, RPP's were found to stimulate decay at

higher concentrations. However, the role of RPP's varied considerably between the physiological groups and individual species models. In three of the individual species (Pacific silver fir, ponderosa pine, and Oregon white oak) models, higher levels of RPP's were associated with slower decomposition (i.e. a negative correlation). Heal et al. (1978) found that two litters with the highest water-soluble tannin concentrations had both the largest and smallest rates of decomposition, suggesting that tannins may have different roles in different plants. The fact that greater concentrations of water-soluble condensed tannins were associated with a reduction of decomposition for the all-species model further demonstrates the high variability in the relationship between tannin concentrations and decay.

These differences in correlations may be due to our inability to differentiate the functional role of tannins with traditional analytical techniques. The BuOH-HCl assay for condensed tannins measures for flavonoid structures colorimetrically. These flavonoid structures however, are not tested for their reactive ability but are assumed to be reactive based on their structure. Testing the reactive ability of the hot water filtrate with casein should provide a better assessment of reactive function, but may not give consistent result with all species examined because of the differences in phenolic functions between and within species.

The individual correlations and regressions with each species analyzed separately demonstrated that no one substrate quality predictor could equally

explain decomposition for all the species studied. Overall, lignin-associated traits and tannin fractions were better predictors than nitrogen and nitrogen-associated ratios. There were also cases where essential nutrients played a key predictive role instead of lignin or tannins. P was found to be an important predictor with red alder, Douglas-fir, ponderosa pine and Pacific dogwood, and Mg and K were important in predicting the decay of Douglas-fir.

This demonstrates that the factors that limit decomposition in this study depend on the quality of the starting material, which not only changes from species to species but within species. This suggests that the spatial scale associated with a decomposition study design substantially influences the results. Thus, the important predictive factors will be different between larger studies that seek to make predictions on a landscape scale and smaller studies focused on the prediction of one species in one forest type.

The relationships discussed above may apply within the same climate, however, when predicting litter decay rates across climates, different factors many become important. Some larger, multiclimate studies have suggested that actual evapotranspiration (AET) is the best predictor across varying climates (Meentemeyer 1978, Aerts 1997) with individual species decay being influenced both by the litter quality and soil nutrient availability. The National Science Foundation Long-Term Intersite Decomposition Experiment Team (LIDET 1995) has shown that litter decay rates of one species in a variety of climatic environments (boreal, temperature and tropical forests) are best

predicted by an interaction between climate and litter chemistry (M. E. Harmon per. comm.). This suggests that predicting global decomposition patterns must be based on more than just the litter quality or climate alone.

Decomposition Experiment

When compared with other decomposition studies using the same Pacific Northwest species, annual decay rates in this study were generally in the same range as that reported by others (Table 11). As expected, conifers had the slowest decay while dogwood and vine maple had the fastest. It was however, a surprise to see how tightly grouped the species were within physiological and morphological classes, especially the nitrogen fixers (Figure 2). These patterns are likely the result of the similar chemistries within each of the four physiological grouping.

Ponderosa pine had higher decay rates in this study than it did in the Hart et al. (1992) and Monleon and Cromack (1996) studies. In Oregon ponderosa pine is found primarily on the east side of the Cascade Mountain range, though there are remnant populations in the Willamette Valley (Franklin and Dyrness, 1973). We were interested in ponderosa pine, as well as Pacific madrone and chinkapin because of the likelihood that these tree species would migrate during a warming climate (Franklin et al. 1991, Neilson and Chaney 1997) and to attempt to understand the potential nutrient inputs to western Cascade soils under different vegetation types. The higher ponderosa pine

decay observed in this study can be explained by the fact that the H. J. Andrews site had greater moisture availability than the sites chosen by Hart et al. (1992) and Monleon and Cromack (1996).

Of the studies listed in Table 11, the Harmon et al. (1990) study had the most similar species selection. In their study of litter decomposition on the Olympic Peninsula, the decomposition rates were generally higher than in this study which is most likely the result of greater annual rainfall, warmer temperatures, and greater summer precipitation at the Olympic Peninsula site. In another experiment on the H. J. Andrews, M. E. Harmon (per. comm.) found very similar values to this study.

Table 11. Comparison of litter decay (K) between this and other studies in the Pacific Northwest.

Species	k-value this study	k-value other studies	Reference
bigleaf maple	0.34 (0.02)[1]	0.67 to 0.69	Harmon et al. 1990
		0.33	Harmon per. comm.
Douglas-fir	0.27 (0.02)	0.29 to 0.39	Harmon et al. 1990
		0.63	Edmonds 1980
		0.48 to 0.56	Edmonds 1979
		0.22 to 0.31	Fogel & Cromack 1977
		0.40	Harmon per. comm.
golden chinkapin	0.54 (0.12)		
Oregon white oak	0.31 (0.01)		
Pacific dogwood	1.02 (0.02)	2.35 to 2.47	Harmon et al. 1990
		0.92	Harmon per. comm.
Pacific madrone	0.39 (0.02)		
Pacific silver fir	0.36 (0.01)	0.45	Edmonds 1980
ponderosa pine	0.31 (0.01)	0.15 to 0.28	Monleon & Cromack 1996
		0.08 to 0.18	Hart et al 1992
poplar	0.34 (0.02)	0.61 to 0.68	Harmon et al. 1990
red alder	0.60 (0.04)	0.47 to 0.93	Harmon et al. 1990
rhododendron	0.49 (0.02)	0.56	Harmon per. comm.
salal	0.41 (0.03)		
Sitka alder	0.56 (0.01)		
snowbrush	0.54 (0.01)		
vine maple	0.82 (0.02)	0.87	Harmon et al. 1990
		0.65	Harmon per. comm.
western redcedar	0.27 (0.01)	0.29 to 0.39	Harmon et al. 1990

1= Standard error in parentheses.

Methodological Considerations

Litterbag Studies

The one mm litterbag mesh size used in this study is common to other decomposition studies making it possible to compare decay rates between studies. The size however does have some drawbacks because it can exclude the litter shredding macroorganisms and can allow foreign material to enter the bag and increase the mass (Schlesinger and Hasey 1981). Thus, the decay values reported here may not be the same as those of litter decomposing outside a litterbag (McCune and Daly 1994). Additionally, because of annual fluctuations in climatic conditions the decomposition rates are likely to vary between years as is litter chemistry (Findlay 1996, Taylor and Parkinson 1988).

The influence of the underlying native litter also has an effect on the decomposition of the confined litter in the bag. It should be considered in decomposition research and is especially important in site selection. Chadwick et al. (1998) demonstrated that native litters with higher concentrations of N and Ca resulted in approximately 15% greater decomposition of the confined litter. The native litter was hypothesized to transport nutrients to the confined *Pinus sylvestris* litter in litterbags by hyphal translocation and leaching of the native litter that had fallen on top of the litterbags. During their study, the pine litter in the litterbags increased in concentrations of N, Ca, P, K, Mg and had a faster decomposition rate.

The presence of several litter types in one litterbag also influences litter decomposition rates and should also be considered. Litter mixing has been tested by Fyles and Fyles (1992), Klemmedson (1992), Blair et al. (1990), Wardle et al. (1997) and McTiernan et al. (1997) and their results suggests that there is often a positive effect on rate of decomposition from mixed litter, though it is not often additive. This is likely the result of changes in the decomposer communities present in the bags with mixed litter and of the differences in litter qualities (Blair et al. 1990). In this study, the lower quality from the high lignin values of the native Douglas-fir litter found on the forest floor of our study site may slow the decay of some of the higher quality litter in the litterbags.

Chemical Analyses

The measurement of RPP's, water and acid-insoluble condensed tannins and acid-soluble lignin offer significant additions to the litter quality information available with proximate analysis.

In this study, we hoped to expand proximate analysis to include measurement of cutin and actual lignin, with the addition of the triethylene glycol procedure (Step 4 and 5), however their were difficulties with these procedures. The rationale for the procedure 4 was to further extract the acid-insoluble residue operationally known as the "Klason lignin" fraction, leaving cutin and insoluble minerals as a residue, and solubilizing and removing actual

lignin. When this procedure was performed it was difficult to rinse all of the triethylene glycol off the crucibles resulting in a post-extraction weight that was more than the original weight. The procedure seems to work well with a larger mass in the extraction crucible, however because the analysis is sequential, larger crucibles were needed to be able to increase the mass in the NPE extraction. Larger crucibles would keep the proportions constant in NPE, PE, and Klason acid extractions and increase the size of the pellet that went into Step 4. Maheswaran and Attiwill (1987) used this procedure successfully but the extraction was carried out in a centrifuge tube instead of a Gooch crucible. Others have used potassium permanganate (Gallardo and Merino 1993) to digest lignin from residual cutin or have used ^{13}C NMR (Preston et. al. 1997) to fractionate the acid-insoluble residue.

There was also a problem with the choice of a standard for the condensed tannin assays. Using a purified standard for each species is recommended (Caroline Preston per. comm.) because it reduces baseline interference problems and should result in more precise absorbance peaks for each tannin. In this study, the published extinction coefficients value for condensed tannins was used to calculate the values (Bate-Smith 1973) and a commercial cyanidin was found to not work well for a wide range of species.

Statistical Approach

Decomposition data can be analyzed in many ways. It is most common to include all the species studied into one regression equation (see Table 1), but it is equally valid to look at each species separately.

Decomposition data can also be analyzed with a either a linear (see Table 1) or a non-linear approach (Mellilo et al 1982, Flanagan and Van Cleve 1983, Harmon et al. 1990, Aerts and de Caluwe 1997, Scott and Binkley 1997, Gallardo and Merino 1993). Gallardo and Merino (1993) compared the results of linear and non-linear models and showed that the significance of the coefficients often increases with the non-linear model but the overall correlation values are generally the same using both approaches. Additionally, the non-linear approach is more difficult to interpret. Others have considered different models for different time periods of decomposition, i.e. for short-term and longer-term studies. While this was only a one year study, work on longer studies often uses a two stage model (Berg and Agren 1984, Harmon et al. 1990, Aerts and de Caluwe 1997). Some have also used multivariate statistics (Heal et al. 1978) and this may help when there are strong correlations between the independent variables. Clearly the questions of interest regarding the spatial and temporals scales of the study should direct many of these choices.

In this study, the goal was to discover if one or a set of predictors could be found that could explain decomposition well for all species. Because

prediction was the goal, correlation and regression analysis are appropriate techniques. However, some of the data were not perfectly linear, e.g. Klason lignin had a slight asymptotic curve as seen in Figure 4. In this data set, lignin appears to flatten out, suggesting that above 35% lignin, increasing the percentage of lignin does not further reduce the decomposition rates. In this analysis, non-linear models were not examined, but they may be useful to capturing the observed curvature. Second and third order polynomials did not significantly improve the regression with lignin.

This study's questions of interest were directed at a forest ecosystem scale, so an analysis with all the species was appropriate. However, because a secondary goal was to find a predictor that could be applied to each species separately, the use of individual analyses are justified. Additionally, PCA was used as an alternative data analysis method and confirmed the results of the all-species correlation and regression analysis. The examination of the first two PCA components, which were a mixture of all of the highly significant variables, showed that no one or group of variables were superior at explaining the decomposition rates observed.

Future Research

In the future, it would be interesting to study the relationship between litter quality and microbial population levels, species distributions and their metabolic and enzymatic activities. It would also be interesting to address if

compounds measured with proximate analysis actually stimulate or retard decomposition, e.g. is the acid-insoluble residue or "Klason lignin" fraction measured in proximate analysis actually difficult to degrade, etc.? Fungi are responsible for cellulose, hemicellulose and lignin degradation through the production of extracellular enzymes and an enzyme study could be used to address these questions (Dix and Webster 1995). Furthermore, what influence do the other litter quality fractions have on the population dynamics of other decomposers? Some research has already shown that water-soluble tannin concentrations are inhibitory to certain fungi (Dix and Webster 1995, Harrison 1971), but are the water insoluble or acid-insoluble tannins inhibitory to most litter decay fungi or to bacteria?

The studies that have included mixed-litters (Fyles and Fyles 1992, Klemmedson 1992, Blair et al.1990, Wardle et al. 1997, McTiernan et al.1997) have shown a positive interaction of differing litter qualities, but how does this influence the spatial and temporal distribution of microorganisms? And how do microorganisms decompose substrates of differing qualities? Fungi in particular are able to use their hyphae to scavenge through the litter layers both vertically and horizontally for organic and inorganic nutrient sources. This ability has been demonstrated by Chadwick et al. (1998) and they have hypothesized that fungi can utilize differing litter qualities to decompose intermixed litter components faster.

It would also be interesting to study changes in fungal species in relation to litter chemistry, particularly with the compounds from the acid-insoluble residue. Fungal colonization occurs before leaf senescence but is generally limited by summer temperatures, water availability and the presence of leaf inhibitory compounds. In the fall, fungal colonization develops rapidly as temperatures drop and moisture increases. At senescence, most leaves are already well colonized by endophytes and "pioneer" fungi and after leaf drop it becomes difficult for other fungi to get established until the immediate sugar resources are depleted and fungal succession can occur (Dix and Webster 1995).

The influences that climatic conditions have on litter chemistry and decomposition process is another field that would be interesting to study. Various phenolics fractions have been shown to increase during stress from drought (Pizzi and Cameron 1986), UV-B (Caldwell et al. 1989 and Gehrke et al. 1995), elevated CO_2 levels (Norby et al. 1986), light intensity (Waterman et al. 1984), nutrient stresses (Coulson et al. 1960, Waring et al. 1985, Flanagan and Van Cleve 1983) and ozone (Jordan et al. 1991, Findlay et al. 1996). Understanding the influence of plant stress on chemical control of decomposition may lead to a better understanding of how decomposition process may be influenced as a result of climate change.

Conclusions

The addition of water and acid-insoluble condensed tannins, acid-soluble lignin and reactive polyphenolics to the proximate analysis scheme offers a more detailed fractionation of the lignin and polyphenolic constituents than traditional proximate analysis (Ryan et al. 1990). This leads to a greater understanding of annual decomposition dynamics for mixed species forests and of many common tree and shrub leaf litters in the western Oregon.

This study found significant differences in mean decay values and chemical qualities between species. Overall, for the multiple regression analysis with all 16 species, litter decay was best predicted by the acid-insoluble condensed tannins, acid-insoluble residue or "Klason lignin", water-insoluble condensed tannins, Ca and total phenolics: N. The results changed when each species was analyzed separately and when the conifers or rapid decomposers, like vine maple and dogwood, were excluded from the model.

The inclusion of dogwood and vine maple strongly influenced the results and elucidated that the litter from these early successional colonizers and less dominant species are likely to be an important nutrient source for forest soils. Dogwood and vine maple litter was found to have the highest concentrations of Ca, P, total phenolics, RPP's.

The improvements to proximate analysis produced several new variables that were highly significant in predicting decomposition. Analyzing for acid- and water-insoluble condensed tannins fractions are recommended using

purified condensed tannins as a standard from each species of interest. The measurement of RPP's is an easy addition to proximate analysis, however the role of this variable in decomposition research needs further investigation because the signs of the regression coefficients were not consistent between different models of decomposition. In other systems, RPP's may be more important, especially in the tropics where N (Palm and Sanchez 1991) and tannin values are likely to be higher. Recent research by Mesquita et al. (1998) in the tropics has found that acid-insoluble condensed tannins were strongly associated with a reduction in leaf decay rates. Additionally, acid-soluble lignin was another easy addition to proximate analysis and it was a highly significant predictor ($p < 0.0001$) of four decomposition models. However, the triethylene glycol extraction of the lignin pellet needs further development, but given the fact that the acid-insoluble condensed tannins were the best predictor for the all-species model, it seems that it is important to accurately fractionate the acid-insoluble residue and to test the role that cutin has in decomposition (Preston et al. 1997).

In conclusion, the analytical additions to the traditional proximate analysis in this study both improved the range of litter quality variables and have suggested that one year decomposition in a temperate forest ecosystem is best predicted by acid-insoluble condensed tannins or Klason lignin and lignin based predictors.

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