Leaf litter chemistry controls on decomposition of Pacific Northwest trees and woody shrubs[1]

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Abstract: The effects of initial leaf litter chemistry on first-year decomposition rates were studied for 16 common Pacific Northwest conifers, hardwoods, and shrubs at the H.J. Andrews Experimental Forest in western Oregon. Leaf litters were analyzed for C, N, P, K, Ca, Mg, proximate organic fractions (nonpolar, polar, acid-hydrolyzable extractives, acid-hydrolyzable lignin, and acid-unhydrolyzable residue, previously termed "Klason lignin"), and biochemical components (total phenolics, reactive polyphenols, water-soluble carbohydrates, water-soluble proanthocyanidins, and water- and acid-unhydrolyzable proanthocyanidins). By including measurements of reactive and residual phenolic fractions and acid-hydrolyzable lignin, these analytical methods improve upon traditional proximate leaf litter analyses. Significant differences in litter chemistries and decomposition rates were found between species. For all species combined, the 1-year decay rate (k) values had highly significant correlations ($P < 0.001$) with 30 out of the 36 initial chemistry variables tested in this study. The three highest correlations were with acid-unhydrolyzable proanthocyanidins, lignocellulose index, and acid-unhydrolyzable residue ($r = 0.83$, –0.81, –0.80, respectively, with $P < 0.0001$ and $n = 339$). We found that no single litter chemistry variable was a universal predictor of the 1-year k value for each of the individual 16 species studied, though phenolic components were more frequent significant ($P < 0.001$) predictors of decomposition rate.

Résumé : L'effet des caractéristiques chimiques initiales de la litière de feuilles sur le taux de décomposition au cours de la première année a été étudié pour 16 conifères, feuillus et arbustes communs du Pacific Northwest à la forêt expérimentale H.J. Andrews dans l'ouest de l'Oregon. Les litières de feuilles ont été analysées pour C, N, P, K, Ca, Mg, des fractions organiques (produits d'extraction non polaires, polaires et hydrolysables dans l'acide, lignine hydrolysable dans l'acide, résidus non hydrolysables dans l'acide antérieurement qualifiés de « lignine Klason »), et des composantes biochimiques (composés phénoliques totaux, polyphénols réactifs, hydrates de carbone solubles dans l'eau, proanthocyanidines solubles dans l'eau, proanthocyanidines non hydrolysables dans l'eau et proanthocyanidines non hydrolysables dans l'acide). En incluant des mesures des fractions phénoliques, réactives et résiduelles, et de la lignine hydrolysable dans l'acide, ces méthodes analytiques constituent une amélioration par rapport aux analyses immédiates traditionnelles de la litière de feuilles. Il y avait des différences significatives entre les caractéristiques chimiques et les taux de décomposition de la litière des différentes espèces. Pour toutes les espèces combinées, le taux de décomposition pendant la première année (k) était significativement corrélé ($P < 0{,}001$) avec la valeur initiale de 30 des 36 variables chimiques testées dans cette étude. Les trois variables les plus fortement corrélées étaient les proanthocyanidines non hydrolysables dans l'acide, l'indice de lignocellulose et les résidus non hydrolysables dans l'acide ($r = 0{,}83$, –0,81 et –0,80 respectivement avec $P < 0{,}0001$ et $n = 339$). Aucune des variables chimiques de la litière n'était un prédicteur universel de la valeur de k pendant la première année pour chacune des 16 espèces étudiées bien que les composés phénoliques aient été les prédicteurs du taux de décomposition les plus souvent significatifs ($P < 0{,}001$).

Introduction

Decomposition of leaf and needle litter is critical to forest nutrient cycling (Cadisch and Giller 1997). Past attempts to predict litter decomposition rates have examined a range of senescent leaf litter-quality characteristics, including N (Flanagan and Van Cleve 1983), C:N (Edmonds 1980; Taylor et al. 1989), lignin (Waksman and Cordon 1938; Berg 2000), lignin:N (Harmon et al. 1990), ^{13}C nuclear magnetic resonance spectroscopy with cross-polarization and magic-angle spinning (CPMAS NMR) (Preston et al. 2000), or equivalent index, such as acid-unhydrolyzable residue:N (Trofymow et al. 2002). Most of the recent decomposition studies have focused on some estimate of lignin or lignin:N ratio, but a few have considered the potential influence of polyphenol control on decomposition (Fox et al. 1990;

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Loranger et al. 2002). However, none of those studies measured polyphenol reactivity in relation to decomposition.

Polyphenol reactivity is likely to influence litter decomposition rates differently than lignin, because of lignin's biochemical structure and less reactive nature. Lignins may control initial decomposition by physical occlusion of enzymes degrading structural carbohydrates, such as cellulose and hemicellulose (Cadisch and Giller 1997). Polyphenols, however, readily form recalcitrant quasistable complexes, in vitro, with detrital proteins, nucleic acids, polysaccharides, and phospholipids (Zucker 1983; Mole and Waterman 1987). Because these complexed substrates are resistant to hydrolytic enzymes (Zucker 1983), they are thought to slow decomposition, leading to organic matter accumulation in acidic forest soils (Zucker 1983). Tannins occur not only in the plant cell wall (Zucker 1983) but also within the central vacuole and subcellular organelles (Stafford 1988), where, upon cell death, they can react with cytoplasmic proteins and nucleic acids. By comparison, lignins are phenylpropyl polymers and are found only in the plant cell wall.

The significance of reactive polyphenols (RPP) in controlling decomposition and nutrient cycling may have been previously overlooked, because of problems with the analytical procedures. Because protein-complexing activity is inversely related to RPP molecular size and solubility (Spencer et al. 1988), conventional extractions recover only the smaller RPP (Haslam 1989). Widely accepted extraction protocols (Effland 1977; Ryan et al. 1990) use solvents that are inadequate to recover larger RPP polymers (Reed 1986; Hagerman 1988). Furthermore, the acid digestion that occurs in these processes precipitates RPP, waxes (cutin), and minerals, along with the material previously termed "Klason lignin" (Waksman and Cordon 1938), leading to an underestimation of polyphenol concentrations and overestimation of the lignin fraction (Reed 1986; Preston et al. 2000.) In these conventional procedures, lignin is only functionally defined as the residue of acid digestion, but is not actually measured. Acid digestion poses another problem: while most conifer lignin is acid-unhydrolyzable, significant fractions of deciduous lignin are acid-hydrolyzable (Effland 1977), resulting in a digestion that is not appropriate for all plant types.

This study was an attempt to improve first-year litter decomposition predictability based upon traditional litter analysis, first, by more accurately measuring the lignin and phenolic pools, and second, by exploring the reactivity of polyphenols as a mechanism to explain decomposition patterns. The project had two objectives: (*i*) to expand traditional proximate leaf analysis (Ryan et al. 1990) to include measurements of reactive polyphenols, water-insoluble and acid-unhydrolyzable proanthocyanidins (condensed tannins), acid-hydrolyzable lignin, acid-unhydrolyzable lignin, cutin, and residual mineral fractions; and (*ii*) to test effects of traditional and expanded leaf litter chemical analyses on 1-year litter decomposition, using a range of common Pacific Northwest tree and shrub species.

Materials and methods

Leaf collection

Recently senesced leaf material from 16 common Pacific Northwest tree and shrub species (Table 1) was collected from five different sites at a similar elevation (450–500 m) for each species in western Oregon in the fall of 1995. The five different collection sites varied between species, because the 16 species are not always found together. The leaf material was either hand collected from trees or shaken free from stems and branches onto clean plastic tarpaulins. The leaf material, kept separate according to species and five collection sites, was air-dried in a 24 °C laboratory room to a constant mass, and 30-g samples of each were ground (40 mesh) for the chemical analyses. The species and sites were selected to provide a range of chemical qualities (Nilsson et al. 1998), and the species represented four a priori classified groups: conifers; hardwoods and shrubs; dinitrogen fixers; and rapid decomposers (a distinct group observed by Harmon et al. 1990). We included ponderosa pine (*Pinus ponderosa* Dougl. ex Loud.) litter in this study, even though it is primarily found east of the Cascades, as well as Pacific madrone (*Arbutus menziesii* Pursh.) and golden chinkapin (*Castanopsis chrysophylla* (Dougl.) A. DC.) litter, because of the likelihood that these species would become more important under a warming climate scenario.

Decomposition experiment

For 11 of the 16 species, we used five replicate litterbags (20 cm × 20 cm, 0.8-mm nylon mesh) for each of the five sites, each containing 5 g dried leaf material, for a total of 25 litterbags per species. For Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), bigleaf maple (*Acer macrophyllum* Pursh.), Oregon white oak (*Quercus garryana* Dougl.), poplar (*Populus trichocarpa* T. & G.), and red alder (*Alnus rubra* Bong.); however, we used only three replicates for each of the five sites, for a total of 15 litterbags per species. The Douglas-fir and Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) litterbags had two layers of mesh to ensure needle retention. On 18 November 1995, the 350 total litterbags were randomly placed at 2-m intervals along eighteen 20-m transects within a mesic old-growth (460-year-old) mixed Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stand and secured on the forest floor with pin flags. The stand was located at 44°12′54″N, 122°14′57″W, 485-m elevation, within the H. J. Andrews Experimental Forest. Mean annual temperature in this area is 9.6 °C, and mean annual precipitation, mostly falling as rain, is 1869 mm. Habitat type is classified as western hemlock/swordfern (*Polystichum munitum* (Kaulf.) Presl)/Oregon oxalis (*Oxalis oregana* Nutt. ex T. & G.). The soils have been described as fine-loamy, mixed frigid family of Dystric Eutrocrepts (Hawk et al. 1978). After 1 year, litterbags were collected, air-dried in a 24 °C laboratory room, cleaned, and weighed. Decomposition was measured as loss in mass, and the annual decay constant (k) was calculated as

$$[1] \qquad -kt = \ln (X_t/X_o)$$

where X_t is mass remaining after time t (1 year) and X_o is original litter mass (Olson 1963). We used 1-year mass loss values, calculated as the mass fraction remaining, to calculate the 1-year k values for each litter sample. We assume that each sample has followed a single-exponential decay equation during the first year. The use of k has limitations in decomposition studies, given the different phases of decomposition over time and the complexity of substrates (Berg et

Table 1. Mean annual leaf litter decay (*k*) rates for species, in ascending order, and *k* values from other Pacific Northwest studies.

Common name	Scientific name	Species group	*k* value		Study references[b]
			This study[a]	Other studies	
Western redcedar	*Thuja plicata* Donn.	Conifer	0.27 (0.01)	0.29–0.39	Harmon et al. 1990
				0.28	Moore et al. 1999
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco	Conifer	0.27 (0.02)	0.29–0.39	Harmon et al. 1990
				0.22–0.31	Fogel and Cromack 1977
				0.40	Prescott et al. 2000
Ponderosa pine	*Pinus ponderosa* Dougl. ex Loud.	Conifer	0.31 (0.01)	0.15–0.28	Monleon and Cromack 1996
				0.08–0.18	Hart et al. 1992
Oregon white oak	*Quercus garryana* Dougl.	Hardwood	0.31 (0.01)		
Bigleaf maple	*Acer macrophyllum* Pursh.	Hardwood	0.34 (0.02)	0.67–0.69	Harmon et al. 1990
Poplar	*Populus trichocarpa* T. & G.	Hardwood	0.34 (0.02)	0.61–0.68	Harmon et al. 1990
Pacific silver fir	*Abies amabilis* (Dougl.) Forbes	Conifer	0.36 (0.01)	0.45	Edmonds 1980
Pacific madrone	*Arbutus menziesii* Pursh.	Hardwood	0.39 (0.02)		
Salal	*Gaultheria shallon* Pursh.	Shrub	0.41 (0.03)		
Rhododendron	*Rhododendron macrophyllum* G. Don	Shrub	0.49 (0.02)	0.56	M.E. Harmon, personal communication
Golden chinkapin	*Castanopsis chrysophylla* (Dougl.) A. DC.	Hardwood	0.54 (0.12)		
Snowbrush	*Ceanothus velutinus* Dougl. ex Hook.	N_2 fixer	0.54 (0.01)		
Sitka alder	*Alnus sinuata* (Reg.) Rydb.	N_2 fixer	0.56 (0.01)		
Red alder	*Alnus rubra* Bong.	N_2 fixer	0.60 (0.04)	0.47–0.93	Harmon et al. 1990
				0.44	Prescott et al. 2000
Vine maple	*Acer circinatum* Pursh.	Rapid decomposer	0.82 (0.02)	0.87	Harmon et al. 1990
				0.65	M.E. Harmon, personal communication
Pacific dogwood	*Cornus nuttallii* Aud. ex T. & G.	Rapid decomposer	1.02 (0.02)	2.35–2.47	Harmon et al. 1990
				0.92	M.E. Harmon, personal communication
LSD[c]			0.06		

[a]Standard error in parentheses.
[b]Litter decay (*k*) values for Douglas-fir and red alder were estimated from first-year mass loss graphical values given in Prescott et al. (2000) and a mass remaining percentage value given for western redcedar by Moore et al. (1999), assuming exponential decay (Olson 1963).
[c]LSD, least significant differences for mean separation, df = (16, 323), $\alpha = 0.05$.

al. 2001). Trofymow et al. (2002) found the single exponential decay equation to be useful in predicting mass remaining over a long-term, 6-year study of 11 species at 18 Canadian sites.

Differences between air-dried and oven-dried (50 °C, 8 h) mass were approximately 5%, as determined by weighing litter subsamples from all the species. Transport loss of material from litterbags between study site and laboratory averaged 1.2% (range: 0.5%–3.4%). Both of these differences were small, so we did not correct for them when calculating the decay values.

Litter quality analysis

For the analyses, the air-dried and previously ground litter samples were oven-dried (50 °C, 4 h). Figure 1 shows the analytical sequence.

Elemental analysis

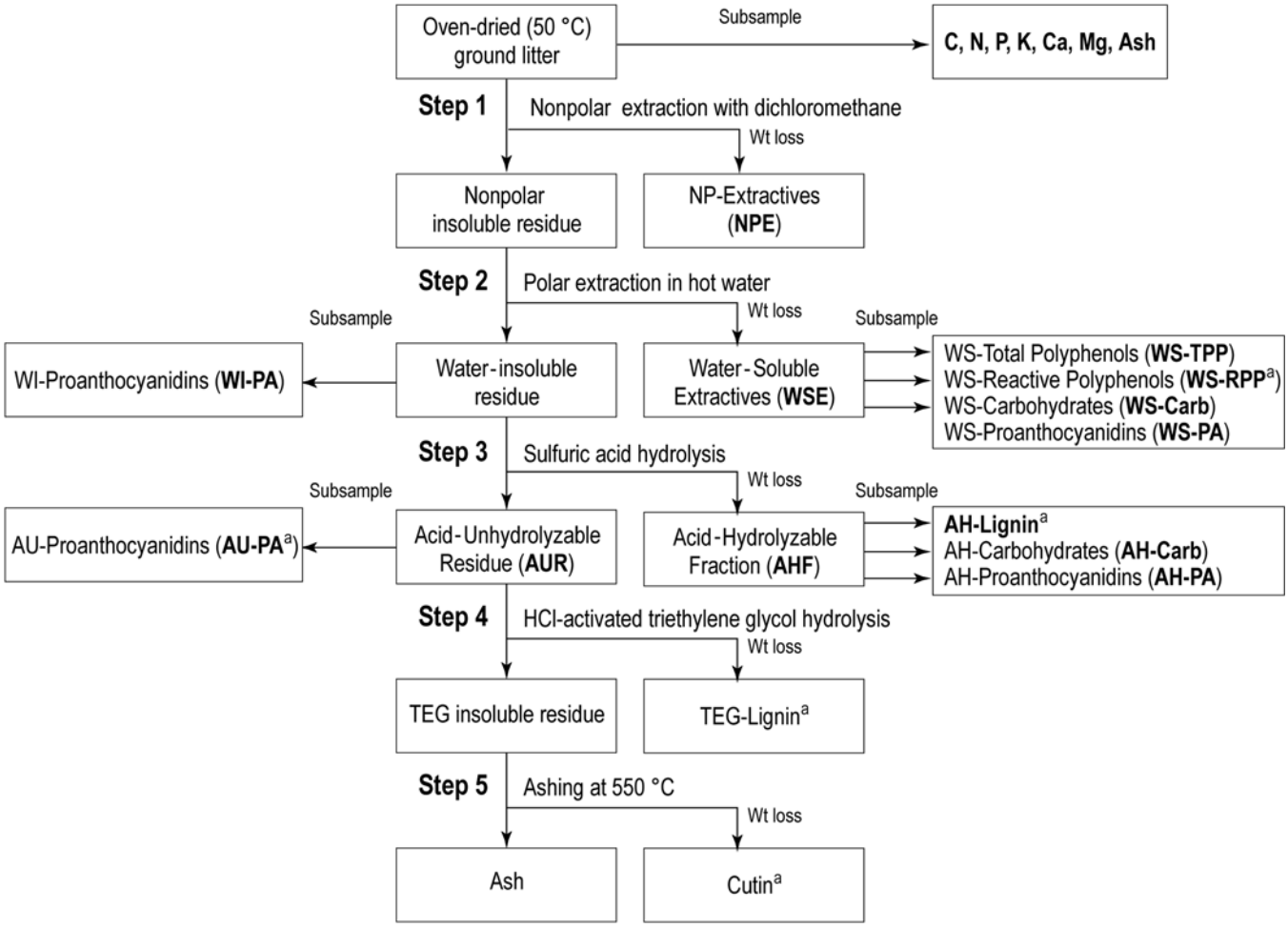
For this procedure, 0.3-g subsamples of the ground, oven-dried material were analyzed for C and N content with a LECO CNS Analyzer (LECO Corp., St. Joseph, Michigan). Additional 0.3-g subsamples of the ground, oven-dried leaf litter were digested individually in 5 mL of concentrated 72% H_2SO_4, followed by 10 sequential additions of 0.25 mL of 30% H_2SO_4 totaling 2.5 mL (Thomas et al. 1967). The digest was diluted in deionized (DI) H_2O to 250 mL and analyzed for P using an ALPKEM autoanalyzer (Beaverton, Oregon) and analyzed for K, Ca, and Mg using atomic absorption spectroscopy with a Perkin-Elmer 5000 (Norwalk, Connecticut). One-gram subsamples were placed in a muffle furnace at 550 °C overnight to determine the ash fraction. These ash concentrations were not used in the expanded proximate analysis and are presented as additional data.

Proximate analysis

We modified the proximate analysis scheme of Ryan et al. (1990) to provide fractions for chemical analysis of water and acid extractions (e.g., total and reactive polyphenols) (see Fig. 1).

Nonpolar extractives were determined as mass loss by dichloromethane extraction. Duplicate 1-g samples of the ground,

Fig. 1. Sequential extraction diagram for the litter-quality analysis. To the right or left of each step in the proximate analysis are the gravimetric and colorimetric fractions measured at that step. Terms in bold are the abbreviations for the elements, proximate fractions, or biochemical compounds used in the data analysis. The "a" indicates those fractions or compounds representing additions from this study to the proximate analysis scheme of Ryan et al. (1990).



oven-dried leaf material were placed in oven-dried and preweighed 30-mL Gooch crucibles and sonicated in 30 mL dichloromethane in a 100-mL beaker for 30 min, after which the filtrate was removed with light suction and washed with 10 mL dichloromethane. The sonication and filtrate removal procedure was repeated three times. Crucibles with residual pellets were air-dried for 1 h and oven-dried at 50 °C for 4 h, then weighed to determine nonpolar extractive mass loss. The crucibles with pellets were then stored in a desiccator (to prevent moisture absorption) until the polar extractive procedure.

Water-soluble extractives (WSE) were estimated as mass loss by hot-water extraction. The weighed nonpolar extractive pellets were transferred to 30-mL centrifuge tubes with a rubber spatula, taking care not to damage the crucible frit. Twenty-five millilitres DI H_2O was added, after which each tube was covered with aluminum foil, vortexed, and steamed for 1 h. The supernatant was then filtered through a weighed crucible into an Ehrlenmeyer flask. This procedure was repeated three times. In the Ehrlenmeyer flask, the combined supernatant was brought to 300 mL with DI H_2O. A 50-mL subsample of this filtrate solution was frozen immediately for the chemical analyses that followed this proximate analysis.

Since we planned to include polyphenols and RPP in the proximate analysis, we needed to confirm that a hot-water extraction was as efficient for polyphenols as the more common 70% aqueous acetone (Hagerman 1988) or 50% aqueous methanol (Gray 1978) extraction processes, since the use of organic solvents would have compromised the polysaccharide determination. Preliminary tests on bigleaf maple, Douglas-fir, Oregon white oak, poplar, and red alder nonpolar extractive residues showed no significant yield difference in extracted polyphenols (Julkunen-Titto 1985) or proanthocyanidins (Porter et al. 1986) for three 1-h steam bath treatments vs. 70% aqueous acetone extractions. Both of these produced higher yields than a 1-h steaming or 50% aqueous methanol extraction.

Acid-hydrolyzable fraction (AHF) and acid-unhydrolyzable residue (AUR) fractions were calculated as mass loss and residual mass loss after acid hydrolysis, respectively, but not on an ash-free basis. Muffle furnace ash concentrations were determined in separate subsamples of ground, oven-dried leaf litter. Weighed WSE pellets were transferred to 20 mm × 150 mm screw-top test tubes. Six millilitres of 72% sulfuric acid was then added to each tube. After the tubes were

vortexed, they were incubated in a 30 °C water bath and vortexed again every 15 min. After 1 h, 18-mL DI H_2O was added to each tube, and the tube contents were transferred to 250-mL Ehrlenmeyer flasks, using 150 mL DI H_2O to rinse. The flasks were capped with aluminum foil and autoclaved for 1 h. After cooling and filtering through a weighed crucible, the filtrates were brought up to 300 mL with DI H_2O. A 10-mL subsample of each was immediately frozen for later analysis of acid-hydrolyzable carbohydrates and lignin. The crucible with residue was oven-dried and weighed; the mass loss was designated as the AHF and the residual mass as the AUR, previously termed "Klason lignin."

Cutin and residual ash fractions were determined as residual mass after hydrolysis with HCl-activated triethylene glycol (TEG) and mass after ignition at 550 °C, respectively. Weighed acid-unhydrolyzable residues (generally under 250 mg) were placed in 20 mm × 150 mm screw-top test tubes. Ten millilitres of activated TEG (3.2 mL of 37% HCl in 500 mL TEG) was pipetted into tubes. Tubes were capped, vortexed, and autoclaved for 1 h at 121 °C (Edwards 1973). After cooling, tubes were vortexed again. Edwards (1973) used three,10-mL washes of 95% EtOH to rinse tubes through a tared Gooch crucible under light suction, followed by two washes of 10 mL acetone. We found this insufficient to remove residual TEG and used several more washes with both solvents until the crucible was visibly clean. The crucibles with residue were oven-dried, weighed, and then ashed (550 °C) to determine cutin (by mass loss) and the mineral residue, or ash. The mass loss in this procedure was designated the TEG-soluble lignin fraction (Edwards 1973). This step was difficult to duplicate consistently because of the small size of the AUR and the difficulty in washing the TEG residues off the crucible. We therefore did not include the results for cutin or residual ash (as diagrammed in the last part of Fig. 1) in our data set and statistical analysis. The residual ash component in the AUR has been used to present AUR on an ash-free basis where feasible (Trofymow et al. 2002).

Chemical analysis

Except for the water-insoluble and acid-unhydrolyzable proanthocyanidin assays, we used DI H_2O blanks to compensate for the absorbance of the filtrate in all of the assays described next.

Total polyphenols (TPP) were determined in diluted (1:10) WSE solution from the hot-water extract with the Folin-Ciocalteau reagent (Julkunen-Titto 1985) using a catechol (1,2-dihydroxybenzene) standard. Reactive polyphenols (RPP) were estimated as the polyphenols precipitated by shaking 3 mL of polar extractives (PE) (diluted 1:10 with DI H_20) to give 30 mL of diluted solution. To this solution was added 150 mg of Sigma purified casein powder prior to shaking for 3 h (adapted from Kuiters and Denneman 1987). After centrifugation, the supernatant was re-assayed for polyphenols. The difference between the pre-casein and post-casein values was designated as the RPP fraction. Water-soluble proanthocyanidins (WS-PA) in the PE filtrate were determined with the butanol–HCl colorimetric reaction (Porter et al. 1986) at 520 nm, modified for incubation in a steam bath. In this assay, even heating between the tubes, as well as choice of a standard, is very important. Water-insoluble (WI-PA) and acid-unhydrolyzable proanthocyanidins (AU-PA) were measured using the methods of Porter et al. (1986) and Reed (1986) on 30–50 mg of water- and acid-extracted pellets, respectively. Water-soluble and acid-hydrolyzable carbohydrates (WS- and AH-CARB) were determined in diluted (1:10) hot-water extract and acid-digest supernatant with a phenol-sulfuric acid reaction (Dubois et al. 1956), using a glucose standard. Acid-hydrolyzable lignin (AH-lignin) was determined by absorbance at 205 nm (Wood and Kellogg 1988) in diluted (1:10) acid supernatant.

Statistical methods

All statistical analyses were performed using SAS version 6.12 (SAS 1994). Differences between species in annual decay rate (k) were tested using one-way analysis of variance (ANOVA). Species differences for the litter chemical characters were tested with one-way ANOVA, with separation of means by Fisher's Protected Least Significant Difference (LSD) at $P = 0.05$.

Linear correlation analysis was used to determine how well individual litter-quality characters predicted k values for each species separately, for the four species groups (conifers, hardwoods and shrubs, dinitrogen fixers, and rapid decomposers) and for all species together. Analysis of residuals showed that assumptions of constant and homogeneous variance were met and no influential outliers were present (Zar 1999). In total, 36 independent variables were assessed for their predictive abilities, including variables from the standard proximate analysis, those from our additions to the proximate analysis, and those reported by others to predict 1-year litter decomposition rates. The 36 predictors were sorted and ranked based upon the r and P-value obtained from the correlation analysis for each litter-quality variable.

Multiple linear regression analysis with stepwise model selection ($P = 0.05$) was used to determine which set of litter-quality characters best predicted the k value for all species together (Zar 1999). The stepwise model was chosen because it employs both the addition and the elimination of independent variables (Zar 1999), with a minimum significance for entry into the model and to stay in the model at $P \leq 0.05$. Independent variables were tested for significant multicollinearity ($P \leq 0.05$), as stepwise selection allows multicollinearity to remain in multiple regression models (Zar 1999). This may affect traditional interpretation of regression coefficients (Zar 1999; Graham 2003). Multiple regression models were constructed for the all-species multiple regression model and for two other species group multiple regression models. This provided an opportunity to evaluate the effects of leaving out the rapid decomposer species group or the conifer species group from the regression analyses.

As an alternative method to the multiple regression model, principal components analysis (PCA) was used (SAS 1994). This method was warranted because it creates linear combinations of the variables that are independent of each other and these combinations reflect which variables explain the overall variation in the data set.

Results

Decomposition

Annual decay rates (Table 1) were significantly different among several of the 16 species ($P < 0.05$). The rapid

Table 2. Elemental analysis of initial leaf litter chemistry by species (n = 5).

Species group	Species	C (%)	N (%)	P ($mg \cdot g^{-1}$)	Ca ($mg \cdot g^{-1}$)	K ($mg \cdot g^{-1}$)	Mg($mg \cdot g^{-1}$)
N_2 fixers	Red alder	50.00 (0.12)	2.13 (0.12)	1.08 (0.08)	9.87 (0.83)	7.23 (0.39)	2.14 (0.18)
	Sitka alder	49.88 (0.14)	2.44 (0.06)	1.83 (0.14)	10.89 (0.95)	3.30 (0.17)	2.60 (0.26)
	Snowbrush	53.02 (0.23)	1.40 (0.09)	0.80 (0.07)	9.19 (1.22)	5.51 (0.57)	1.61 (0.22)
Conifers	Douglas-fir	51.62 (0.07)	0.52 (0.02)	0.70 (0.03)	10.89 (0.30)	0.56 (0.12)	0.92 (0.13)
	Pacific silver fir	51.92 (0.29)	0.37 (0.02)	0.57 (0.07)	10.53 (1.96)	1.58 (0.35)	1.33 (0.17)
	Ponderosa pine	51.98 (0.21)	0.64 (0.07)	0.91 (0.11)	3.88 (0.40)	3.91 (0.72)	1.83 (0.12)
	Western redcedar	52.56 (0.30)	0.46 (0.03)	0.56 (0.03)	23.45 (1.71)	3.27 (0.60)	1.05 (0.09)
Hardwoods and shrubs	Bigleaf maple	47.42 (0.42)	0.81 (0.10)	2.18 (0.14)	18.48 (1.61)	6.26 (0.41)	2.49 (0.63)
	Golden chinkapin	52.22 (0.22)	0.47 (0.08)	0.43 (0.03)	6.98 (0.77)	1.77 (0.20)	1.32 (0.13)
	Oregon white oak	48.14 (0.32)	1.49 (0.12)	2.06 (0.23)	15.91 (1.28)	3.75 (0.27)	1.96 (0.08)
	Pacific madrone	50.50 (0.33)	0.49 (0.16)	1.00 (0.09)	10.87 (1.80)	3.53 (0.81)	2.56 (0.39)
	Poplar	46.64 (0.62)	0.80 (0.18)	2.03 (0.30)	18.56 (2.60)	8.57 (0.77)	1.99 (0.26)
	Rhododendron	51.34 (0.40)	0.33 (0.02)	0.56 (0.06)	12.35 (0.81)	5.60 (0.43)	2.51 (0.22)
	Salal	49.74 (0.30)	0.44 (0.02)	0.41 (0.03)	16.11 (0.59)	3.40 (0.31)	3.87 (0.20)
Rapid decomposers	Pacific dogwood	45.26 (0.21)	0.69 (0.04)	5.03 (0.31)	26.13 (1.89)	6.75 (0.65)	3.66 (0.12)
	Vine maple	44.76 (0.73)	0.94 (0.11)	2.91 (0.65)	15.45 (1.50)	7.57 (1.44)	5.53 (0.50)
LSD[a]		0.99	0.26	0.61	3.98	1.7	0.78

Note: Means with standard errors in parentheses.
[a]LSD, least significant difference for mean separations, df = (16, 64), α = 0.05.

decomposer group had the highest rates (k = 1.02 for Pacific dogwood (*Cornus nuttallii* Aud. ex T. & G.) and 0.82 for vine maple (*Acer circinatum* Pursh.)). Lowest decay rates were found in two conifer species (k = 0.27), with Pacific silver fir having the highest conifer rate (k = 0.36). Decay for the hardwood trees and shrubs group and the dinitrogen fixers generally fell somewhere between the conifers and the rapid decomposers.

Litter quality

Overall, there were both within- and between-species variations in the initial litter chemistry data, and some patterns existed, following some of the species groupings. To analyze the within-species variation, we used the mean and standard error to calculate coefficients of variation (CV) (Zar 1999) for each litter-quality variable, expressed as a percentage of the mean. We found that initial litter C (Table 2) had the smallest within-species variation (CV range from 0.32% to 3.66%), as compared to N, for example, which had much higher within-species variation (CV range from 5.25% to 70.63%). Analysis of the initial litter elemental composition (Table 2) also showed between-species variation and patterns by species groups, especially for N and P. The highest N concentrations were found in the two alder species and the highest P concentrations occurred in the rapid decomposers.

Our modified proximate analysis (Table 3) also revealed some distinctive patterns among species groups, as did the carbohydrate, polyphenol, and proanthocyanidin analyses (Table 4). The proximate factors, such as NPE, PE, AUR (Table 3), and carbohydrate fractions and proanthocyanidins (Table 4), all had more consistent patterns of variability, with a CV range of approximately 5%–30%. Reactive polyphenols (RPP) had some of the largest variations in concentration, with individual species CV values of 90.55% (for bigleaf maple, for example) (Table 4).

In Table 5, ratios of variables from Tables 2–4, some of which have previously been shown to be useful predictors of decay, are displayed with use of AUR, the updated term for the "Klason lignin" fraction. These ratios — C:N (Taylor et al. 1989), C:P, RPP:N, TPP:N, TPP:P, AUR:P, and AUR:N (Harmon et al. 1990) — have the advantage of combining both the negative influence of inhibitory compounds (e.g., C compounds) in the numerator and the positive influence of stimulatory factors (e.g., N or P) in the denominator. A variety of acid unhydrolyzable-based ratios are also given in Table 5: lignocellulose index (AUR:[AUR + AH-CARB] (Melillo et al. 1989)); AUR + PP:N (Fox et al. 1990); AUR:WS-CARB; and TPP:WS-CARB). Litter chemistry ratios (Table 5) exhibit a greater range in variation, depending upon the ratio index, with RPP:N exhibiting the greatest range in CV (11%–113%).

Initial litter-quality predictors of decomposition

We used 36 predictors to test linear correlations of initial litter chemistry and decomposition rates of all 16 species. The results of a simple linear correlation analysis between the k values and each predictor appear in the bottom row of Table 6. Thirty of the variables (with r = 0.19) showed highly significant correlations ($P < 0.001$). The four variables with the strongest correlations were: AU-PA (r = 0.83); AUR (r = –0.80); the lignocellulose index (r = –0.81); and total lignin (AUR + AH-lignin) (r = –0.72). Each of these four variables explains at least 50% of the variation in k values, and the next 12 variables explain at least 25% of the variation. Reactive polyphenols were a mid-range predictor (r = 0.54) of decomposition, as was AUR:N (r = –0.58), both substantially better than N (r = 0.19) or C:N (r = –0.29). Acid-hydrolyzable lignin (r = 0.67) was a mid-range predictor, but with a positive correlation to k.

Examining correlations for individual species (Table 6) reveals no single litter chemistry variable as a universal predictor for all species. The highest frequency of correlation was found with four variables (WSE, RPP, AU-PA, and P), each of which were significantly ($P < 0.01$) correlated to k

Table 3. Expanded proximate analysis of initial leaf litter chemistry by species (n = 5).

(A) Leaf litter chemistry analysis part 1.

Species group	Species	Ash (%)	NPE (%)	WSE (%)	WSE + NPE (%)
N_2 fixers	Red alder	4.54 (0.33)	5.02 (0.29)	39.47 (1.05)	44.49 (1.13)
	Sitka alder	4.28 (0.18)	5.49 (0.33)	28.95 (0.50)	34.44 (0.64)
	Snowbrush	3.36 (0.43)	7.04 (0.10)	44.79 (1.37)	51.83 (1.35)
Conifers	Douglas-fir	6.43 (0.14)	10.99 (0.31)	14.87 (1.23)	25.87 (1.27)
	Pacific silver fir	3.94 (0.35)	10.40 (0.83)	37.61 (0.89)	48.01 (1.13)
	Ponderosa pine	3.52 (0.38)	8.87 (0.27)	22.13 (0.80)	31.00 (0.88)
	Western redcedar	6.41 (0.53)	10.80 (0.68)	26.26 (0.66)	37.06 (0.89)
Hardwoods and shrubs	Bigleaf maple	9.62 (0.47)	8.86 (0.54)	19.81 (1.72)	28.67 (1.61)
	Golden chinkapin	2.57 (0.39)	5.64 (0.36)	31.08 (1.25)	36.72 (1.27)
	Oregon white oak	6.72 (0.44)	4.33 (0.14)	24.09 (0.80)	28.42 (0.87)
	Pacific madrone	4.32 (0.35)	4.56 (0.41)	39.59 (2.46)	44.16 (2.73)
	Poplar	9.36 (0.82)	6.49 (0.26)	32.58 (1.87)	39.07 (1.94)
	Rhododendron	4.39 (0.14)	5.50 (0.57)	32.45 (2.29)	37.95 (2.77)
	Salal	6.24 (0.20)	5.43 (0.26)	29.07 (1.18)	34.50 (1.40)
Rapid decomposers	Pacific dogwood	10.98 (0.33)	6.19 (0.16)	48.53 (0.94)	54.72 (1.03)
	Vine maple	10.20 (0.79)	7.27 (0.86)	36.75 (1.36)	44.02 (1.91)
LSD[b]		1.23	1.30	3.90	4.38

(B) Leaf litter chemistry analysis part 2.

			Acid-unhydrolyzable residue (%)		
Species group	Species	AH[a] fractions (%)	AUR	AH-lignin	AUR + AH-lignin
N_2 fixers	Red alder	36.23 (0.74)	19.27 (0.66)	5.75 (0.22)	25.03 (0.61)
	Sitka alder	40.77 (0.86)	24.79 (0.51)	5.86 (0.26)	30.65 (0.50)
	Snowbrush	31.26 (0.48)	16.91 (1.31)	3.89 (0.10)	20.80 (1.36)
Conifers	Douglas-fir	39.94 (0.57)	34.19 (1.22)	0.76 (0.07)	34.96 (1.24)
	Pacific silver fir	30.02 (0.68)	21.97 (0.79)	1.81 (0.05)	23.78 (0.77)
	Ponderosa pine	40.30 (0.74)	28.70 (0.46)	1.17 (0.07)	29.87 (0.47)
	Western redcedar	36.47 (0.84)	26.47 (0.76)	1.57 (0.04)	28.04 (0.73)
Hardwoods and shrubs	Bigleaf maple	45.93 (0.96)	25.40 (1.16)	2.07 (0.12)	27.47 (1.13)
	Golden chinkapin	41.99 (0.99)	21.30 (0.53)	2.29 (0.06)	23.59 (0.58)
	Oregon white oak	42.77 (0.39)	28.81 (0.82)	2.01 (0.11)	30.82 (0.78)
	Pacific madrone	35.39 (0.83)	20.46 (2.46)	4.19 (0.18)	24.65 (2.63)
	Poplar	39.11 (1.16)	21.82 (1.36)	1.69 (0.32)	23.52 (1.37)
	Rhododendron	40.76 (1.75)	21.29 (1.14)	2.21 (0.21)	23.50 (0.96)
	Salal	43.70 (0.56)	21.79 (0.98)	1.18 (0.02)	22.97 (0.98)
Rapid decomposers	Pacific dogwood	39.06 (0.95)	6.22 (0.47)	6.54 (0.52)	12.76 (0.74)
	Vine maple	41.91 (1.92)	14.07 (0.17)	3.35 (0.18)	17.41 (0.19)
LSD[b]		2.79	2.99	0.57	3.06

Note: Means with standard errors in parentheses. NPE, nonpolar extractives; WSE, water-soluble extractives; AH, acid-hydrolyzable fractions; AUR, acid-unhydrolyzable residue.

[a]Acid-hydrolyzable (AH) fractions include sugars from hydrolyzed cellulose and hemicellulose and acid-hydrolyzable lignin (AH-lignin).

[b]Least significant difference for mean separations, df = (16, 64), α = 0.05.

for four different species. Fractions or ratios that included acid-unhydrolyzable residue and proanthocyanidins generally were better predictors than N and N-based ratios. Two of the best predictors for all species combined, AU-PA and AUR, are presented graphically in Figs. 2 and 3, together with the linear regression equations for each of these predictive variables.

To test the influence of the clustering associated with the species groups (Figs. 2 and 3), particularly for the rapid decomposer group and for the conifers, we expanded the analysis to examine the relationship between average decay rates for each species group and the independent chemistry variables. We also performed analyses on all groups together, excluding the rapid decomposers in one case and the conifers in another (Table 6). These analyses revealed only one variable that predicted the decomposition rates of the dinitrogen fixer group, lignocellulose index (r = –0.34), whereas for the conifers, hardwoods, and rapid decomposers, many variables were correlated with the decay rates. WS-CARB had the highest correlation with the conifer group (r = 0.69); ash and TPP:P were best correlated with the hardwood group (r = –0.5 and r = 0.5, respectively); and AH-lignin was the highest correlate with the rapid decomposers (r = 0.70). Without the rapid decomposers, AH-lignin (r = 0.56), followed closely by AUR

Table 4. Initial carbohydrate, polyphenol, and proanthocyanidin concentrations by species (n = 5).

(A) Initial carbohydrate and polyphenol concentrations.

		Carbohydrates[a]			Polyphenols[b]	
Species group	Species	WS-CARB	AH-CARB	WS + AH	WS-RPP	WS-TPP
N_2 fixers	Red alder	148.64 (9.76)	363.40 (24.83)	512.04 (21.81)	63.64 (3.45)	87.22 (3.50)
	Sitka alder	82.89 (8.97)	451.66 (6.47)	534.55 (10.10)	36.92 (1.38)	48.94 (1.78)
	Snowbrush	145.43 (12.72)	319.76 (5.21)	465.19 (16.57)	68.82 (3.14)	87.44 (3.36)
Conifers	Douglas-fir	68.17 (3.72)	413.69 (10.44)	481.86 (10.53)	10.55 (1.20)	20.37 (1.77)
	Pacific silver fir	172.25 (15.56)	356.22 (13.09)	528.47 (18.11)	42.08 (3.89)	56.75 (3.36)
	Ponderosa pine	101.57 (2.89)	605.23 (9.11)	706.80 (9.38)	12.26 (2.64)	25.24 (2.89)
	Western redcedar	86.85 (5.83)	420.38 (12.43)	507.24 (9.59)	30.06 (2.36)	42.39 (2.55)
Hardwoods and shrubs	Bigleaf maple	77.53 (6.38)	457.63 (20.10)	535.16 (24.26)	12.14 (4.91)	23.10 (5.20)
	Golden chinkapin	79.69 (1.30)	444.61 (16.77)	524.30 (16.19)	54.56 (4.98)	69.34 (5.31)
	Oregon white oak	63.41 (2.24)	416.71 (9.56)	480.13 (11.00)	34.96 (3.35)	44.86 (3.49)
	Pacific madrone	92.72 (12.90)	365.85 (24.35)	458.58 (29.89)	57.90 (6.79)	80.32 (8.72)
	Poplar	133.13 (16.82)	429.13 (15.44)	562.27 (24.73)	32.11 (5.15)	45.81 (4.79)
	Rhododendron	79.02 (1.33)	441.47 (16.15)	520.49 (15.50)	35.34 (4.65)	53.99 (6.07)
	Salal	92.77 (12.83)	366.79 (22.99)	459.56 (28.91)	34.95 (2.81)	46.11 (3.08)
Rapid decomposers	Pacific dogwood	107.75 (9.03)	594.08 (11.05)	701.83 (17.64)	69.69 (4.22)	96.44 (4.60)
	Vine maple	87.25 (1.20)	608.68 (23.47)	695.93 (22.42)	44.29 (7.46)	61.19 (8.36)
LSD[d]		26.56	46.17	53.97	12.00	13.40

(B) Initial proanthocyanidin concentrations.

		Proanthocyanidins (%)[c]				
Species group	Species	WS-PA	WI-PA	AU-PA	WI + AU	WS + WI + AU
N_2 fixers	Red alder	0.24 (0.02)	5.20 (0.20)	4.16 (0.09)	9.36 (0.26)	9.60 (0.25)
	Sitka alder	0.26 (0.02)	11.98 (0.58)	12.15 (0.63)	24.13 (0.94)	24.39 (0.96)
	Snowbrush	1.12 (0.06)	22.92 (0.92)	6.87 (0.34)	29.79 (0.94)	30.90 (0.98)
Conifers	Douglas-fir	0.45 (0.05)	9.11 (0.78)	3.05 (0.20)	12.16 (0.96)	12.61 (0.99)
	Pacific silver fir	1.57 (0.14)	11.63 (1.70)	2.99 (0.19)	14.62 (1.85)	16.19 (1.89)
	Ponderosa pine	0.54 (0.11)	8.50 (0.84)	3.72 (0.21)	12.22 (0.95)	12.76 (1.03)
	Western redcedar	1.05 (0.07)	7.70 (0.23)	3.46 (0.14)	11.16 (0.35)	12.20 (0.37)
Hardwoods and shrubs	Bigleaf maple	0.47 (0.07)	8.28 (1.53)	4.01 (0.46)	12.29 (1.95)	12.76 (2.02)
	Golden chinkapin	0.79 (0.06)	7.49 (0.46)	5.96 (0.25)	13.45 (0.69)	14.24 (0.68)
	Oregon white oak	0.31 (0.05)	3.88 (0.35)	1.59 (0.02)	5.47 (0.35)	5.78 (0.40)
	Pacific madrone	0.70 (0.08)	8.50 (0.94)	6.55 (0.65)	15.05 (1.58)	15.75 (1.56)
	Poplar	1.15 (0.22)	13.00 (1.70)	0.36 (0.03)	13.36 (1.73)	14.51 (1.62)
	Rhododendron	1.14 (0.10)	18.37 (0.93)	12.10 (0.67)	30.48 (1.38)	31.62 (1.40)
	Salal	1.70 (0.12)	12.80 (1.27)	7.87 (0.20)	20.67 (1.26)	22.38 (1.34)
Rapid decomposers	Pacific dogwood	0.12 (0.01)	2.53 (0.09)	24.07 (1.55)	26.59 (1.62)	26.72 (1.62)
	Vine maple	0.21 (0.04)	4.70 (1.00)	15.44 (1.02)	20.14 (1.93)	20.35 (1.97)
LSD[d]		0.26	2.77	1.63	3.67	3.72

Note: Means with standard errors in parentheses.

[a]Milligrams glucose equivalents per gram for water-soluble (WS-CARB) and acid-hydrolyzable (AH-CARB) carbohydrates.

[b]Milligrams catechol equivalents per gram for water-soluble reactive polyphenols (WS-RPP) and water-soluble total polyphenols (WS-TPP).

[c]Proanthocyanidins are calculated using the extinction coefficient of 150 (Bate-Smith 1973) for water-soluble (WS-PA), water-insoluble (WI-PA), and acid-unhydrolyzable (AU-PA) proanthocyanidins.

[d]Least significant difference for mean separations, df = (16, 64), α = 0.05.

(r = 0.54), had the highest overall correlations with k for the all-species grouping. Without conifers, the highest correlation for the all-species grouping was with WI-PA (r = 0.80).

A stepwise multiple regression model representing the best set of litter-quality variables for all species combined is summarized in Table 7. A multiple regression equation was constructed using individual species k values, obtained from eq. 1, as the dependent variable and litter-quality variables as independent variables. This model is as follows:

$$[2] \quad -k = 1.03\ (0.04) + 0.02\ (0.001)\ \text{AU-PA} - 0.02\ (0.001)\ \text{AUR} - 0.01\ (0.001)\ \text{WI-PA} - 0.06\ (0.008)\ \text{Ca} - 0.06\ (0.008)\ \text{PP:N}$$

where R^2 = 0.84, P = 0.0001, n = 339, and SE is shown in parentheses.

In this model, AU-PA accounted for 68%, AUR accounted for 9%, and WI-PA, Ca, and PP:N each accounted for 2% of

Table 5. Predictive indices of initial leaf litter quality for each species (n = 5).

(A) Predictive indices part 1.

Species group	Species	C:N	C:P	N:P	RPP:N	TPP:N	TPP:P
N_2 fixers	Red alder	23.79 (1.17)	474.52 (45.12)	20.06 (1.81)	3.06 (0.29)	4.18 (0.34)	83.18 (9.87)
	Sitka alder	20.47 (0.48)	279.75 (20.71)	13.77 (1.27)	1.52 (0.07)	2.01 (0.10)	27.29 (1.77)
	Snowbrush	38.47 (2.44)	682.15 (55.28)	17.65 (0.48)	5.04 (0.53)	6.40 (0.64)	113.65 (12.92)
Conifers	Douglas-fir	98.88 (3.06)	740.70 (30.06)	7.53 (0.46)	2.02 (0.23)	3.90 (0.35)	28.84 (1.49)
	Pacific silver fir	142.84 (9.55)	967.13 (118.21)	7.11 (1.30)	11.70 (1.59)	15.74 (1.74)	104.26 (11.87)
	Ponderosa pine	84.73 (8.83)	608.38 (77.42)	7.15 (0.34)	2.14 (0.61)	4.27 (0.87)	30.97 (6.86)
	Western redcedar	116.49 (7.10)	947.79 (57.95)	8.14 (0.13)	6.68 (0.69)	9.42 (0.87)	76.91 (7.62)
Hardwoods and shrubs	Bigleaf maple	61.50 (6.04)	220.90 (14.76)	3.81 (0.60)	1.75 (0.88)	3.17 (1.04)	10.35 (1.94)
	Golden chinkapin	119.51 (15.20)	1234.54 (97.93)	10.96 (1.47)	12.95 (2.48)	16.39 (2.99)	165.82 (21.29)
	Oregon white oak	33.14 (2.59)	243.43 (23.15)	7.52 (0.86)	2.47 (0.40)	3.15 (0.45)	22.85 (3.33)
	Pacific madrone	141.22 (31.94)	523.94 (50.95)	5.06 (1.65)	17.82 (5.02)	24.53 (6.87)	84.01 (14.62)
	Poplar	70.89 (15.23)	253.33 (40.38)	4.54 (1.44)	5.35 (1.86)	7.32 (2.19)	23.98 (3.03)
	Rhododendron	155.88 (10.03)	956.83 (108.43)	6.07 (0.33)	10.92 (1.87)	16.64 (2.57)	103.31 (19.78)
	Salal	114.09 (3.60)	1231.28 (88.25)	10.83 (0.79)	7.98 (0.58)	10.54 (0.65)	112.90 (6.47)
Rapid decomposers	Pacific dogwood	66.09 (3.53)	91.37 (5.62)	1.42 (0.16)	10.22 (0.96)	14.13 (1.18)	19.32 (0.90)
	Vine maple	49.83 (5.21)	197.43 (52.55)	3.85 (0.79)	5.09 (1.14)	6.99 (1.37)	28.57 (9.57)
LSD[a]		30.92	182.36	2.88	4.77	6.22	29.39

(B) Predictive indices part 2.

Species group	Species	AUR:P	AUR:N	(AUR + TPP):N	LCI	AUR:WS-CARB	TPP:WS-CARB
N_2 fixers	Red alder	182.85 (17.97)	9.15 (0.45)	13.33 (0.76)	0.35 (0.02)	1.33 (0.14)	0.60 (0.06)
	Sitka alder	138.74 (9.58)	10.18 (0.37)	12.19 (0.42)	0.35 (0.01)	3.16 (0.41)	0.61 (0.05)
	Snowbrush	212.72 (9.82)	12.03 (0.32)	18.43 (0.56)	0.34 (0.02)	1.21 (0.16)	0.62 (0.04)
Conifers	Douglas-fir	493.27 (36.96)	65.34 (2.10)	69.24 (1.87)	0.45 (0.01)	5.11 (0.44)	0.30 (0.01)
	Pacific silver fir	412.67 (59.69)	60.12 (3.28)	75.86 (5.01)	0.38 (0.02)	1.32 (0.14)	0.35 (0.05)
	Ponderosa pine	334.78 (40.68)	46.61 (4.51)	50.88 (5.31)	0.32 (0.01)	2.84 (0.10)	0.25 (0.03)
	Western redcedar	475.44 (23.81)	58.45 (3.02)	67.88 (3.63)	0.39 (0.01)	3.10 (0.24)	0.50 (0.04)
Hardwoods and shrubs	Bigleaf maple	118.79 (10.76)	32.66 (2.75)	35.83 (3.26)	0.36 (0.02)	3.37 (0.34)	0.30 (0.07)
	Golden chinkapin	503.02 (39.93)	48.22 (5.31)	64.60 (8.27)	0.32 (0.01)	2.68 (0.10)	0.87 (0.07)
	Oregon white oak	145.79 (14.06)	19.68 (1.10)	22.83 (1.55)	0.41 (0.01)	4.58 (0.29)	0.71 (0.05)
	Pacific madrone	209.51 (26.36)	51.30 (8.14)	75.83 (14.69)	0.36 (0.04)	2.40 (0.45)	0.93 (0.15)
	Poplar	121.02 (24.08)	33.01 (6.81)	40.33 (8.75)	0.34 (0.02)	1.78 (0.30)	0.36 (0.04)
	Rhododendron	392.77 (41.95)	64.30 (4.26)	80.94 (5.29)	0.33 (0.02)	2.70 (0.17)	0.68 (0.07)
	Salal	545.18 (63.00)	49.90 (2.35)	60.44 (1.99)	0.37 (0.02)	2.52 (0.33)	0.55 (0.09)
Rapid decomposers	Pacific dogwood	12.68 (1.54)	8.94 (0.17)	23.08 (1.17)	0.09 (0.01)	0.60 (0.09)	0.92 (0.08)
	Vine maple	61.72 (16.24)	15.62 (1.56)	22.61 (2.78)	0.19 (0.01)	1.61 (0.03)	0.70 (0.09)
LSD[a]		91.65	10.50	15.57	0.05	0.76	0.19

Note: Means with standard errors in parentheses. RPP, reactive polyphenols; TPP, total polyphenols; AUR, acid-unhydrolyzable residue; (AUR + PP):N, Fox et al. (1990) index; LCI, lignocellulose index (AUR:AUR + AH-CARB); WS-CARB, water-soluble carbohydrates.

[a]Least significant difference for mean separations, df = (16, 64), α = 0.05.

the variation in the decay (no other variables provided explanation of any more variability). Each independent variable was highly significant (Table 7). The two most important variables in the model are AU-PA and AUR (see Figs. 2 and 3), which have two of the highest correlation coefficients for individual litter chemistry variables (Table 6). These two variables are significantly correlated (r = –0.75, $P < 0.01$), thus diminishing the utility of this regression model (Zar 1999; Graham 2003), even though the five litter-quality variables were highly significant and the model had a high R^2 (Table 7). Either of the individual linear regression models for AU-PA and AUR, as given in Figs. 2 and 3, may be better predictive tools, and appear to be stronger statistically than the multiple regression model (eq. 2), with significant (r = 0.75, $P < 0.01$) multicollinearity between AU-PA and AUR (Zar 1999).

Multiple linear regression models run for each species and for the same groups of species as listed in Table 6 also found no one set of predictors could explain decomposition for all groups. To test the influence of the rapid decomposers, a

Table 6. Correlations (r) of decay (k) and leaf-litter chemistry for individual species, species groups, and all species together ($P < 0.01$).

(A) Correlations part 1.

				Extractives[a]				AUR and AH-lignin[b]		
Species group	Species	n	Ash	NPE	WSE	NPE + WSE	AH	AUR	AH-lignin	AUR + AH-lignin
N_2 fixers	Red alder	13								
	Sitka alder	24								
	Snowbrush	25			0.50			–0.56		–0.56
Conifers	Douglas-fir	15			0.69	0.70		–0.62		
	Pacific silver fir	25			0.64	0.68	–0.68			
	Ponderosa pine	24			–0.63	–0.66	**0.79**			
	Western redcedar	23								
Hardwoods and shrubs	Bigleaf maple	15							**–0.75**	
	Golden chinkapin	25								
	Oregon white oak	15								
	Pacific madrone	24								
	Poplar	14								
	Rhododendron	25								
	Salal	23		0.52				–0.60	–0.53	–0.61
Rapid decomposers	Pacific dogwood	24								
	Vine maple	25								
N_2 fixers		62								
Conifers		87	–0.48		0.55	0.51	–0.44	–0.53	0.37	–0.54
Hardwoods and shrubs		141	–0.50					–0.36		–0.37
Rapid decomposers		49			0.62	0.47		–0.65	0.70	–0.53
Without rapid decomposers		290	–0.41	–0.44	0.46	0.34		–0.54	0.56	–0.38
Without conifers		252	0.40	0.19	0.57	0.59		**–0.78**	0.57	–0.67
All species[f]		339	0.41	–0.30	0.62	0.56		–0.80	0.67	–0.72

(B) Correlations part 2.

Species group	Species	n	C	N	P	K	Ca	Mg	C:N	C:P
N_2 fixers	Red alder	13			–0.67					0.68
	Sitka alder	24								
	Snowbrush	25								
Conifers	Douglas-fir	15			0.69	0.72		0.71		–0.68
	Pacific silver fir	25				0.70				
	Ponderosa pine	24			0.54					
	Western redcedar	23								
Hardwoods and shrubs	Bigleaf maple	15								
	Golden chinkapin	25								
	Oregon white oak	15								
	Pacific madrone	24								
	Poplar	14								
	Rhododendron	25								
	Salal	23						–0.58		
Rapid decomposers	Pacific dogwood	24			–0.55					0.56
	Vine maple	25								
N_2 fixers		62								
Conifers		87					–0.37	0.28		
Hardwoods and shrubs		141	0.49	–0.37	–0.48	–0.25	–0.48		0.36	0.47
Rapid decomposers		49		–0.37			0.44	–0.55	0.38	
Without rapid decomposers		290		0.41		0.17	–0.33	0.16	–0.20	
Without conifers		252	–0.45		0.61	–0.29	0.33	0.43	–0.20	–0.32
All species[f]		339	–0.57	0.19	0.65	0.43	0.26	0.56	–0.29	–0.39

Note: For individual species group values, values ≥0.75 or ≤–0.75 are in bold.
[a]NPE, nonpolar extractives; WSE, water-soluble extractives.
[b]AUR, acid-unhydrolyzable residue (previously termed "Klason lignin"); AH-lignin, acid-hydrolyzable lignin.
[c]Milligrams glucose equivalents per gram for water-soluble (WS-CARB) and acid-hydrolyzable (AH-CARB) carbohydrates.
[d]Milligrams catechol equivalents per gram for water-soluble reactive polyphenols (WS-RPP) and water-soluble total polyphenols (WS-TPP).
[e]Percent per sample. WS, water-soluble; WI, water-insoluble; AU, acid-unhydrolyzable.
[f]For all species combined, all correlation (r) values ($P < 0.001$) were highly significant; correlation values ($r = 0.12$) are considered significant at $P < 0.05$.
[g]RPP, reactive polyphenols.
[h]TPP, total polyphenols.
[i]LCI, lignocellulose index [(AUR: (AUR + AH-CARB)].

Table 6 (*concluded*).

Carbohydrates[c]			Polyphenols[d]		Proanthocyanidins[e]				
WS	AH	WS + AH	WS-TPP	WS-RPP	WS-PA	WI-PA	AU-PA	WI + AU	WS + WI + AU
	0.65						0.63		
0.67			0.65	0.64					
0.61		0.51		–0.52					
	0.73	0.73	–0.60	–0.57	–0.55	–0.53	–0.73	–0.64	–0.65
0.54									
			–0.61	–0.61					
						–0.55	–0.64	–0.59	–0.61
	0.48	0.50							
						–0.59	0.61		
0.69			0.29		0.28	0.38	0.32	0.31	0.33
	0.24	0.24	0.27	0.26			0.38	0.23	0.24
0.42			0.49	0.44	–0.48	–0.41	0.66	0.54	0.53
0.18			0.51	0.50		0.26	0.50	0.40	0.39
0.17	0.66	0.73	0.47	0.43	–0.47	–0.37	**0.80**	0.35	0.31
	0.47	0.47	0.58	0.54	–0.43	–0.26	0.83	0.47	0.44

N:P	AUR:N	RPP[g]:N	TPP[h]:N	(AUR + TPP):N	LCI[i]	AUR:WS-CARB	TPP:CARB	TPP:P	AUR:P
								0.66	0.68
	–0.63				–0.60				
	–0.65	0.64	0.64			–0.66			–0.66
						–0.64	–0.56		
–0.68				–0.68			–0.60		
						–0.54	–0.62		–0.54
0.54		–0.56	–0.56	–0.58					
					–0.34				
–0.33		0.29	0.34			–0.62	–0.39		–0.45
0.24	0.33	0.28	0.28	0.33	–0.37	–0.29		0.50	0.39
–0.38	–0.57	–0.44	0.47		–0.62	–0.64			–0.41
0.53	–0.41			0.30	–0.38	–0.39	0.31	0.34	–0.19
–0.19	–0.45			–0.33	**–0.81**	–0.60	0.27	–0.20	–0.40
–0.12	–0.58			–0.45	–0.81	–0.57	0.44	–0.12	–0.52

multiple regression model of decomposition without the rapid decomposers (Table 6) was examined. The results of this analysis suggest that the inclusion of these species (with low acid-unhydrolyzable concentrations) influences the predictive models. This multiple regression model found that AH-lignin, AUR, N:P, and AU-PA were significant predictor variables, with an overall lower correlation than the all-species model (R^2 = 0.49, P < 0.001, n = 290). As above, the AUR and AU-PA variables are significantly correlated (r = –0.75, P < 0.01), and may diminish the utility of the multiple regression (Zar 1999; Graham 2003).

To test the influence of the conifer group on the all-species model, a model without the conifers was examined. In this multiple regression model, lignocellulose index, AU-PA, and N:P produced the best fit (R^2 = 0.80, P < 0.001, n = 252). However, lignocellulose and AU-PA are collinear (r = –0.85,

Fig. 2. Species group patterns showing a significant linear regression ($P < 0.0001$, $n = 339$) between the acid-unhydrolyzable proanthocyanidins (AU-PA) and decay rate (k).

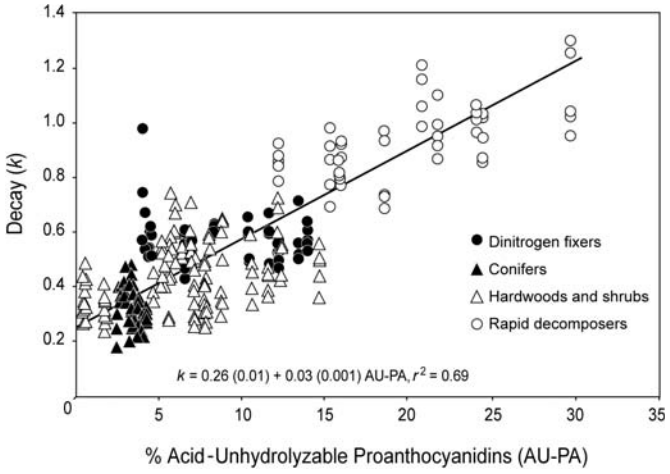
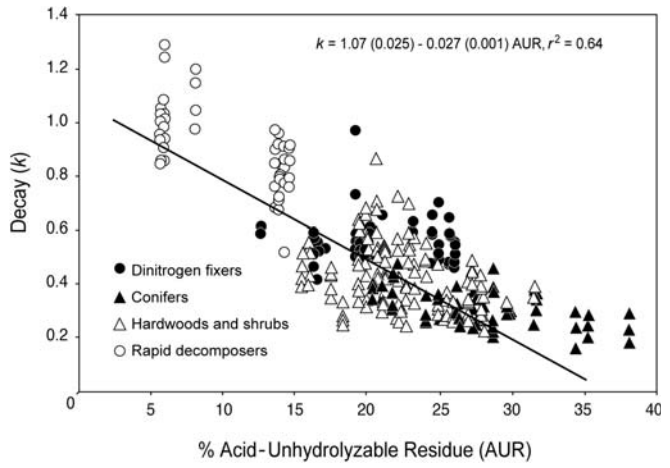


Fig. 3. Species group patterns showing a significant linear regression ($P < 0.0001$, $n = 339$) between acid-unhydrolyzable residue (AUR) and decay rate (k).



$P < 0.001$), thus limiting statistical application of this model (Zar 1999; Graham 2003). As individual variables, lignocellulose ($r = –0.81$) and AU-PA ($r = 0.80$) were almost equally correlated with decay rates for the group of species without conifers (Table 6).

PCA was used independently to check the results of the multiple regression analysis for the all-species multiple regression model given in Table 7. This analysis suggested that the first six eigenvectors accounted for 87% and the first 27 eigenvectors accounted for 99% of the variation in the 36 independent variables (data not shown). Though the eigenvectors were not easily interpretable, the first principal component was a ratio of the lignin variables to the AU-PA, polar extractive, and P variables, which accounted for 35% of the variation. The PCA permitted separation of lignin variables and the AU-PA, in contrast to significant multicollinearity effects in the multiple regression model results given above. The second principal component was a contrast of the total polyphenols:P, RPP:N, and total polyphenols:N variables to the AHF and the AH-CARB fractions. This accounted for an additional 22% of the variation.

A second data set that excluded the 12 variables that were ratios of the independent variables was also tested (data not shown). The results of the two PCAs were very similar. This second analysis suggested that the first six 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, whereas the second principal component was a contrast of water-insoluble proanthocyanidins and C to the acid hydrolyzables and the acid-hydrolyzable carbohydrate fractions.

Discussion

Decomposition experiment

As expected, conifers had lower decay rates than broadleaved species, with dogwood and vine maple (or rapid decomposer group) having the highest. Except for Pacific silver fir, decay rates followed species grouping patterns (Table 1), especially for the dinitrogen fixers. We surmise that this phenomenon likely results from the similar chemistries and leaf or needle morphologies within each of the four groupings in the present study.

The 1-year decay rate constants for the leaf material in our study were generally in the same range as reported by others (Table 1). The lower decay rates for ponderosa pine found by Hart et al. (1992) and Monleon and Cromack (1996) are likely to be the result of lower moisture availability at their study sites than ours. On the other hand, the slightly higher decomposition rates from the Harmon et al. (1990) study are likely the result of greater annual rainfall, summer precipitation, and higher temperatures in the Olympic Peninsula. The k values reported by M.E. Harmon (personal communication) were from another experiment on the H.J. Andrews Experimental Forest and, as expected, were very similar to decay rates found in our study.

Initial litter-quality predictions of decomposition

All species combined

Highly significant ($P < 0.001$) linear correlations for litter decay rates were found for 30 of the 36 predictors when all plant species were analyzed together (last line in Table 6). As the best predictors, AU-PA, lignocellulose index, AUR, and total lignin (or AUR + AH-lignin) each explained at least 50% of decomposition variation. These variables were strong predictors of decomposition because they include an assessment of the amorphous AUR, which frequently has been associated with recalcitrant litter components and the buildup of forest humus (Berg et al. 2001). A long-term decomposition study by Trofymow et al. (2002), involving 11 litter substrates and 18 sites across Canada, found several litter-quality variables (including AUR and AUR:N, together with temperature and summer precipitation) over a 6-year time span. In their study, a variety of litter-quality variables and winter precipitation were important in predicting decomposition within the first year. The single-exponential decay model worked reasonably well for both 1-year and 6-year re-

Table 7. ANOVA from the all-species multiple regression model with decay (*k*).

(A) Overall ANOVA results.[a]					
Source	df	Sum of squares	Mean square	*F* value	*P* >*F*
Model	5	14.00578	2.80116	373.029	0.0001
Error	333	2.50057	0.00751		
Total	338	16.50636			
(B) Parameter estimates.					
Variable	df	Mean	SE	*t*	*P* >|*t*|
Intercept	1	1.03	0.041	24.823	0.0001
Acid-unhydrolyzable proanthocyanidin	1	0.02	0.001	13.818	0.0001
Acid-unhydrolyzable residue	1	–0.02	0.001	–17.59	0.0001
Water-insoluble proanthocyanidin	1	–0.01	0.001	–8.276	0.0001
Ca	1	–0.06	0.008	–7.729	0.0001
Total polyphenols : N	1	–0.06	0.008	–7.729	0.0001

[a]Root MSE = 0.08666; dependent mean = –0.48973; R^2 = 0.8485; adjusted R^2 = 0.8462.

sults, though not as well for some species during the first year (Trofymow et al. 2002).

Twelve other predictors explained between 25% and 50% of the decomposition variations. These include P and Mg, which are essential nutrients; PP, total-CARB, total extractives, and AH-lignin, which are easily leached and higher-carbon-based nutrients; and several previously used lignin-based ratios of decomposition, including AUR:N, AUR:P, and AUR:WS-CARB. The remaining predictors each explained less than 25% of the decay rate variation, although some of these variables had been previously found to predict decomposition, including C:N (Edmonds 1980; Taylor et al. 1989), N (Flanagan and Van Cleve 1983), and TPP:N (Palm and Sanchez 1991; Aerts and de Caluwe 1997).

The lower correlation (r = –0.29) between decay rates and C:N is probably due to the wide range of forms and decomposability of these elements in plant material. For example, the C in AH-lignin is more recalcitrant than the C in AH-CARB. Cotrufo et al. (1995) have shown the limitation of C:N as a predictor in a study using birch leaves that had widely varying C:N ratios. Initially, their litters had different decay slopes, but after 1 year of decomposition, the net mass loss converged at approximately the same weight. Although N was not a major predictor in our study, it could become more important in the later stages of decomposition if N were to become complexed with residuals (acid-unhydrolyzable fractions) and RPP, thereby reducing the pool of biologically available N (Berg et al. 2001).

In prior studies, lignin:N (Harmon et al. 1990), equivalent to acid-unhydrolyzable residue:N (Trofymow et al. 2002), and total polyphenols:N (Palm and Sanchez 1991; Aerts and de Caluwe 1997) have been found to be good predictors of decomposition. In our study, AUR:N was one of the better predictors (r = –0.58), but TPP:N ratio (r = 0.08) was not. The poor performance of the total TPP:N ratio and the stronger performance of AUR:N suggest that these lignin-like compounds are very influential in the determination of k in temperate forests. This is supported by the tropical research of Palm and Sanchez (1991), who found that the PP:N ratio was a better predictor of N mineralization than lignin:N. Furthermore, in our study there was little difference between AUR:N (r = –0.58) and AUR:P (r = –0.52) in predicting decomposition, which further supports the role of AUR in temperate forest ecosystems. Based on the results of our work with polyphenols, we hypothesize that polyphenols may be stronger controllers in long-term decomposition studies and in the tropics (Mesquita et al. 1998; Loranger et al. 2002), where N and proanthocyanidin concentrations are likely to be higher (Palm and Sanchez 1991) and where decomposition rates generally are higher.

The predictors tested in the present study had both negative and positive correlations with decay. Higher concentrations of AUR-related variables were associated with lower decay rates (i.e., they retarded decay) in the all-species model (see Fig. 3). Fogel and Cromack (1977), Flanagan and Van Cleve (1983), Melillo et al. (1989), and Trofymow et al. (2002) have found similar results. Negative correlations in our study were also found with WS-PA (r = –0.43), nonpolar extractives (r = –0.30), AUR:N (r = –0.58), AUR:WS-CARB (r = –0.57), and AUR:P (r = –0.52). Of these, the relationship between AUR:P and decomposition has also been reported by Gallardo and Merino (1993). These findings suggest that (*i*) litter decomposition rates can be inhibited by higher concentrations of acid-unhydrolyzable residue, probably through the mechanism of physical occlusion of structural carbohydrates such as cellulose (Cadisch and Giller 1997), and (*ii*) the inhibitory nature of lignin in the numerator is stronger than the stimulatory nature of the denominator variable (e.g., P or N). Higher concentrations of leaf litter N, found in dinitrogen fixers such as alders, may inhibit decay in later stages because of the possible inhibition of lignin decay by fungi at higher substrate N concentrations. This is discussed by Berg (2000) in his continued development of the concept of decomposition rate limit values.

Several variables were positively correlated with decay in the all-species model. These included, in descending order of influence, AU-PA (r = 0.83), AH-lignin (r = 0.67), P (r = 0.65), TPP (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 of TPP with decay does not follow the findings of Gallardo and Merino (1993), who found negative relationships between polyphenols and decomposition. In this study, TPP may have accelerated decay because they were quickly leached or used as a C source to stimulate microbial activity.

The positive correlation between k and both the acid-hydrolyzable form of lignin (AH-lignin) and the essential nutrients (P, Mg, K, Ca, and N) were expected. The higher correlation of k with P vs. its lower correlation with N suggests that in the litter components of the H.J. Andrews Experimental Forest, N was abundant and P concentrations may be limiting. The C:P ratio also was a better predictor ($r = –0.39$) than was the C:N ratio ($r = –0.29$). Aerts and de Caluwe (1997) found P to be important in predicting decomposition rates. Magnesium, Ca, and K would be involved in decay because they are essential nutrients for all bacteria and fungi, as is thought for Mn, though this element was not tested in our study. Calcium had a significant correlation ($r = 0.26$, $P < 0.01$) with decomposition as a single variable in the all-species decomposition model (Table 6), and has been shown to influence litter decomposition processes (Berg 2000). Magnesium was significantly correlated ($r = 0.56$, $P < 0.001$) with k for all species combined, in agreement with previous work (Berg 2000).

The high positive correlation between AU-PA and decay in the all-species model is difficult to interpret (Fig. 2). This proanthocyanidin fraction is typically included in the measurement of AUR during proximate analysis and is likely to be attached to the other acid-unhydrolyzable components (e.g., lignin and cutin). Our results differ from those of Mesquita et al. (1998), who found that tropical litter with higher proanthocyanidin concentrations in the neutral-detergent fiber residue (another measurement of lignin) was associated with slower decomposition at 1.5 year. Perhaps the proanthocyanidin assay on the acid-unhydrolyzable residue measures individual flavonoids that are linked into cutin and lignin (which do react with BuOH-HCl), but it lacks the degree of polymerization to complex with cytoplasmic proteins (Spencer et al. 1988). Another possibility is that, as the lignin is degraded, the inhibitory effects of proanthocyanidin on decomposition become enhanced over time, and therefore only a longer study would show proanthocyanidin inhibiting decay (Loranger et al. 2002.) If AU-PA compounds retain their reactive character in later stages of decay, their presence may sequester nutrients, providing an explanation of why N or P concentrations increase in decomposing litter (Melillo et al. 1989).

The positive correlation of k with RPP in the all-species model was not expected. We originally hypothesized a negative correlation, which would confirm the complexing ability of many phenols with N and P compounds to contribute to reduced decomposition rates. Instead, we found that RPP stimulated decay at higher concentrations. However, the role of RPP varied considerably among the species groups and individual species models. For three species models (Pacific silver fir, ponderosa pine, and Oregon white oak), higher levels of RPP were associated with slower decomposition (i.e., a negative correlation). In the study by Heal et al. (1978), the two litters with the highest water-soluble PA concentrations had both the highest and lowest decomposition rates, suggesting that proanthocyanidins may play different roles for different plants. The fact that greater concentrations of WS-PA (a small overall percentage of WI-PA and AU-PA) reduced decomposition for the all-species model further demonstrates the high variability in the relationship between PA concentrations and decay.

A possible explanation for the large differences found in RPP effects on decomposition is that our analytical techniques cannot differentiate between proanthocyanidins with different functional roles. The BuOH–HCl assay for PA reacts with heterocyclic ring oxygen of the flavonoid structures, not with the potentially reactive vicinal dihydroxyl groups on the C-ring. These flavonoid structures, however, are not tested for their reactive ability in the type of analysis we performed, but rather are assumed to be reactive based on their structure. In the future, testing the reactive ability of all the various polyphenol fractions may provide a better assessment of reactive function.

The multiple regression model of the effects of litter-quality variables on all species combined (eq. 2), with limitations resulting from the significant ($P < 0.01$) multicollinearity in our regression model, agrees with Trofymow et al. (2002). Both AUR and AUR:N are significant litter-quality variables affecting first-year litter decomposition when wood is included in their best three-variable multiple regression model. Phenols and water-soluble extractives are significant litter-quality variables when wood is not included in their best three-variable model. After 3 and 6 years, AUR:N is the most important litter-quality variable, together with climatic variables for average annual temperature and precipitation (Trofymow et al. 2002). As in our study, Trofymow et al. (2002) included a wide range of litter quality for the 11 litter types tested.

Previous work using PCA to evaluate the effects of litter-quality variables (Preston et al. 2000) has shown that aromatic C (measured by ^{13}C CPMAS NMR) and AUR form one of the principal components. In our work, AUR was in the first principal component.

Separate analyses for each species

The results of our individual species analyses indicate that no single factor will predict decomposition rates for all species. Rather, the factors that limit decomposition depend on the quality or chemistry of the starting material, which varies not only from species to species, but also within a given species. Therefore, the spatial scale associated with a decomposition study design may substantially influence study results. In other words, the important predictive factors will differ between larger studies that seek to make predictions on a landscape or larger scale, and those smaller studies focused on the prediction at a smaller scale, such as one species in one forest type (Gholz et al. 2000).

Methodological considerations

Chemical analysis considerations

Determination of reactive polyphenolics, water-soluble proanthocyanidins, acid-unhydrolyzable proanthocyanidins, and acid-hydrolyzable lignin offers significant additions to the litter-quality information available through proximate analysis. One of our objectives was to expand proximate analysis to distinguish between cutin and true lignin in the acid-unhydrolyzable fraction, using triethylene glycol (TEG) (Edwards 1973). We found it difficult to rinse the post-reflux TEG residue from the Gooch crucibles in a reproducible manner. The result was sometimes a postextraction mass that was greater than the original mass. Maheswaran and Attiwill (1987) used TEG successfully, but the extraction was carried out in a centri-

fuge tube instead of a Gooch crucible. Others have used potassium permanganate (Gallardo and Merino 1993) to digest lignin selectively from residual cutin, or have used ^{13}C NMR (Preston et al. 2000) to describe the acid-unhydrolyzable residue.

There also was a problem with the standard we used for the proanthocyanidins assays. Using a purified standard for each species is recommended (C. Preston, personal communication) because it reduces baseline interference problems and should result in more precise absorbance peaks for each proanthocyanidin. In this study, however, a commercial anthocyanidin did not work well for a wide range of species, and so the published extinction coefficient for proanthocyanidins (Bate-Smith 1973) was used to calculate the values.

Study design considerations

Decomposition data from multiple species can be analyzed in several ways. It is common to include all the species studied in one regression equation (Edmonds 1980; Harmon et al. 1990). However, Figs. 2 and 3 show species grouping patterns, as have been found by Berg (2000), suggesting that either groups of related species or individual species could be analyzed separately. Others have considered different models for different decomposition time periods, that is, for shorter and longer term studies, which often use two-stage models to distinguish initial and later decay stages (Harmon et al. 1990; Aerts and de Caluwe 1997; Trofymow et al. 2002). Clearly, the questions of interest regarding the spatial and temporal scales of a study should direct many of these choices. One goal of our study was to determine whether a single predictor or related set of predictors could be found to explain annual decomposition for all species together. Because this study was at a forest ecosystem scale, we were interested in obtaining broad, general associations between litter quality and decomposition. However, our results varied greatly when we used one model to predict multiple species decomposition versus separate models for the individual species. For example, as shown by Figs. 2 and 3, the inclusion of Pacific dogwood and vine maple (the rapid decomposer group) significantly influences the shape of our figures and, as a result, our prediction equations. However, including a variety of tree and shrub species, with a substantial range of decay rates, substrate chemistry, and nutrient concentrations, provides a more general basis for testing litter composition and nutrient effects on decomposition rates in a typical temperate forest ecosystem.

With larger scale or even multiclimatic studies, actual evapotranspiration has been shown to be a predictor of decomposition across varying climates (Meentemeyer 1978; Gholz et al. 2000) and should be considered in study design. Results from the Long-Term Intersite Decomposition Experiment Team (LIDET) study found that litter decay rates for two species in a variety of boreal, temperate, and tropical forest environments were best predicted by an interaction between climate and litter chemistry (Gholz et al. 2000). They suggest that leaf litter will decompose more rapidly in its native environment and has a "home-field advantage" over transplanted litter. In a study integrating decomposition of 11 common litter substrates across 18 Canadian sites, Moore et al. (1999) found highly significant multiple regressions (r^2 = 0.64 – 0.73) incorporating lignin:N, mean annual precipitation, and mean annual temperatures. These results enabled them to model litter mass remaining as a result of possible changes, caused by increased atmospheric CO_2, in mean annual temperatures, precipitation, and initial litter chemistry. In another study with soil microarthropods, decomposition was greater when a common leaf litter was placed in two tropical forest environments than when it was placed in a temperate forest, suggesting that decomposition by soil fauna interacts with climate (Heneghan et al. 1999). Overall, these studies suggest that predicting global decomposition patterns should be based on more than just litter quality or climate alone.

Conclusions

Our improved resolution of the lignin and phenolic components in the traditional proximate analysis — through addition of water-insoluble proanthocyanidins, acid-unhydrolyzable proanthocyanidins, acid-hydrolyzable lignin, and reactive polyphenolic fractions — has provided valuable information about how initial chemical qualities of leaf litter influence the 1-year decomposition patterns of common tree and shrub litters in the Pacific Northwest. When all 16 species in this study were combined, we found that 1-year decomposition in this climate had a highly significant relationship with acid-unhydrolyzable proanthocyanidins in addition to the relationship with the acid-unhydrolyzable residue (previously termed "Klason lignin"). Through the exploration of the effects of individual species and species groups we learned that no single litter chemistry variable was a universal predictor of the 1-year decay for each of the individual 16 species studied, though phenolic components were more frequent predictors of decomposition of individual litters. By including a wide variety of tree and shrub species with a substantial range of decay rates and nutrient concentrations, we provide a more general basis for broadly understanding litter-quality effects on 1-year decomposition rates in this temperate forest ecosystem.

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