Influence of initial chemistry on decomposition of foliar litter in contrasting forest types in British Columbia

C.E. Prescott, L. Vesterdal, C.M. Preston, and S.W. Simard

Abstract: We compare rates of decay of foliar litters of British Columbia tree species in two field studies, and assess which initial litter chemistry parameters best predict the decay rates. Nutrient concentrations, tannins, and carbon fractions (based on proximate analysis and nuclear magnetic resonance spectroscopy) were measured in fresh litter of 14 tree species in one experiment and seven species in a second experiment. Each study was replicated in a different site in order to assess the transferability of results. Broadleaf litters decayed faster than needle litters only during the first year; thereafter, they decayed slower. Lignin concentration was a good predictor of mass loss only during the first year and only in one of the two experiments, which may have resulted from all foliar litters having high lignin concentrations (>170 $mg \cdot kg^{-1}$). Litter chemistry effects on first-year decay were consistent and transferable among sites. None of the initial litter chemistry parameters were good predictors of mass remaining after 4 or 5 years, because mass loss of most litters was similar by this time. The convergence in mass losses of litters after 4–5 years despite initial differences indicates that decomposition estimates extrapolated from early rates or initial chemistry may not accurately predict long-term decay.

Résumé : Nous avons comparé le taux de décomposition de la litière de feuilles d'espèces d'arbres de la Colombie-Britannique dans le cadre de deux études sur le terrain et nous avons évalué quels paramètres chimiques initiaux de la litière permettaient le mieux de prédire le taux de décomposition de la litière. La concentration des nutriments ainsi que les proportions de tannins et de carbone (basées sur l'analyse immédiate et la spectroscopie par résonance magnétique nucléaire) ont été mesurées dans la litière fraîche de 14 espèces d'arbres dans une première expérience et de sept espèces dans une deuxième expérience. Chaque étude a été répétée dans un endroit différent pour évaluer la transférabilité des résultats. La litière de feuillus s'est décomposée plus vite que la litière de conifères seulement durant la première année; par la suite, elle s'est décomposée plus lentement. La concentration de lignine était un bon prédicteur de la perte de masse seulement pendant la première année et seulement dans une des deux expériences; ce qui pouvait être dû à la forte concentration (>170 $mg \cdot g^{-1}$) de lignine dans toutes les litières. L'effet des caractéristiques chimiques de la litière sur la décomposition pendant la première année était consistant et transférable parmi les sites. Aucun des paramètres chimiques initiaux de la litière n'était un bon prédicteur de la masse résiduelle après 4 ou 5 ans parce que la perte de masse de la plupart des litières était alors semblable. Cette convergence des pertes de masse de litière après 4 ou 5 ans malgré les différences initiales indique que les estimations de décomposition extrapolées à partir de taux initiaux ou de caractéristiques chimiques initiales ne peuvent prédire avec précision la décomposition à long terme.

[Traduit par la Rédaction]

Introduction

Accurate prediction of litter decay rates is a key requirement of carbon budget and ecosystem models. The two principal determinants of decomposition rates are the climate (temperature and moisture) and the physical and chemical nature or quality of the litter. Litter chemistry has usually been estimated from concentrations of various carbon fractions or nutrients in litter.

The initial lignin content of the litter is often negatively correlated with the rate of decay (Meentemeyer 1978; Taylor et al. 1991; Murphy et al. 1998), with lignin in this case referring to the Klason lignin component, which is the acid-insoluble residue remaining after proximate analysis. Initial litter N concentrations often positively correlate with early decay rates (Berg and Staaf 1980; Taylor et al. 1989; Tian et al. 1992). Positive relationships between decay rates and P concentrations have also been reported at sites where P availability is low either because of edaphic factors or high N deposition (Vitousek et al. 1994; Aerts and De Caluwe 1997; Vesterdal 1999).

Indices that incorporate both C chemistry and nutrient content, such as C:N, lignin:N, or C:P, are often the best predictors of early decay rate (Aerts 1997; Moore et al. 1999;

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Seneviratne 2000). Negative correlations between initial polyphenol concentrations and rates of decomposition or N mineralization have been reported in several studies (Fox et al. 1990; Palm and Sanchez 1991; Loranger et al. 2002). As well, the amount of cutin in litter may be an important determinant of decay rate, as cutin is both highly resistant to decomposition and also related to physical toughness (Gallardo and Merino 1993; Preston et al. 1997). Determination of C fractions in litter by solid-state ^{13}C nuclear magnetic resonance (NMR) spectroscopy has also proven useful in characterizing litter potential to decompose and release nutrients. In particular, the content of alkyl C (waxes and cutin), as determined by NMR, increases during decomposition and may be a useful indicator of litter decomposability (Baldock and Preston 1995). As well, near infrared reflectance (NIR) spectroscopy shows promise for assessing litter decomposability (Gillon et al. 1999; Joffre et al. 2001) and following changes in C fractions during decomposition (Coûteaux et al. 1998).

The influence of litter quality is obvious in the differences in decay rates of various tissue types, but identifying the particular litter characteristic (or combination of characteristics) that is consistently closely related to decomposability has proven surprisingly difficult to do. Across a broad range of litter types, C:N ratio appears to be the best predictor of decay rate (Enriquez et al. 1993; Pérez-Harguindeguy et al. 2000), while within smaller ranges, such as leaf litters, the lignin content or lignin:N ratio is better correlated with decay (Melillo et al. 1989; Harmon et al. 1990; Loranger et al. 2002). Long-term studies have indicated that the factors that best correlate with rates of early decay are often not the same as those that relate to long-term decay (Aber et al. 1990; Coûteaux et al. 1998; Joffre et al. 2001; Yang and Janssen 2002). Berg and Staaf (1980) suggested that early decomposition is regulated by nutrient concentrations (especially N and P), and late-stage decay by lignin concentration. Litter N concentration is often positively related to initial decay rate, but negatively related to the decay rate of more humified materials (Berg et al. 1982; Fog 1988; Saiya-Cork et al. 2002). Initial litter N concentrations are also associated with greater humus accumulation (Berg et al. 2001). A further impediment to finding a consistent predictor of decay rates is the transportability of results. Most studies of litter quality influences have been conducted on a single site, and it is not known if the best predictors of decay rates as determined at one site are transferable to different sites. These inconsistencies and knowledge gaps about the influences of litter quality currently constrain our ability to model C storage and fluxes in soils.

British Columbia has a diversity of climates and, hence, a variety of forest types and tree species. Although the forests are predominantly coniferous, many contain a component of broadleaf species such as *Populus*, *Alnus*, or *Betula*. Broadleaf litter often decomposes faster than needle litter (Cole and Rapp 1981; Cornelissen 1996) and it has been suggested that the rapid decay of broadleaf litter leads to faster nutrient recycling in mixedwood forests (Perry et al. 1987; Simard 1996). However, there is little information on the relative rates of decay of foliar litters of these species or on which litter chemistry parameters are most useful for predicting their decay rates. We addressed this question in two field studies measuring decay rates of foliar litter of (*i*) 14 tree species in coastal British Columbia and (*ii*) 7 species in the Interior Cedar–Hemlock (ICH) biogeoclimatic zone, which contains most of the tree species found in the province. In both experiments, the relationship between litter mass loss and initial litter chemistry was explored through regression analyses, to determine the parameters that best predict decomposition rates of foliar litter in British Columbia forests. To assess the transportability of results, we repeated each study in different environments: the coastal study was repeated in a boreal forest site and the ICH study was conducted in three forests in the ICH and also in adjacent clearcuts at each site. Our hypotheses were as follows:

1. Broadleaf litters decompose faster than needle litters;
2. Relative decomposition rates are predictable from the initial lignin concentration, the lignin:N ratio, or the alkyl-C content of litter;
3. Short- (1-year) and long-term (4- to 5-year) mass losses are not predictable from the same litter chemistry variables;
4. The same litter chemistry variables that best predict rates of decay at one site apply to the same litters at other sites.

Materials and methods

Coastal experiment

Foliar litter of 14 species of trees in British Columbia was collected at sites across the province in the fall of 1993. The 14 species were: lodgepole pine (*Pinus contorta* Dougl.), western white pine (*Pinus monticola* Dougl.), ponderosa pine (*Pinus ponderosa* Laws.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western larch (*Larix occidentalis* Nutt.), Engelmann spruce (*Picea engelmannii* Parry), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), western redcedar (*Thuja plicata* Donn ex. D. Don), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), amabilis fir (*Abies amabilis* (Dougl.) Forbes), trembling aspen (*Populus tremuloides* Michx.), black cottonwood (*Populus trichocarpa* Brayshaw), red alder (*Alnus rubra* Bong.), and vine maple (*Acer circinatum* Pursh). Senesced foliage was collected either from branches just prior to abscission or in plastic trays after abscission. Two grams (dry mass equivalent) of litter was put into litterbags of fiberglass screening with pore size 1.5 mm. The size of the bags varied from 10 cm × 10 cm to 20 cm × 20 cm depending on the size of the leaves. In December 1993, the bags were pinned to the forest floor in a coastal mixed conifer forest at the University of British Columbia Research Forest near Maple Ridge, British Columbia (49°17′N, 122°36′W). The site is at 180 m elevation in the dry maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (CWHdm). Mean annual temperature is 9 °C and average annual precipitation is 2166 mm. The forest was a mature stand of western redcedar, western hemlock, and Douglas-fir.

Bags containing litter of the 10 coniferous species were similarly constructed and installed in September 1993 in a boreal forest dominated by interior spruce (Engelmann (*Picea engelmannii* Parry) × white spruce (*Picea glauca* (Moench) Voss)) near Taylor, British Columbia (55°57′N, 120°36′W, 670-m elevation). The boreal site is in the moist-

warm subzone of the Boreal Black and White Spruce biogeoclimatic subzone (BWBSmw1) (DeLong et al. 1990). Mean annual temperature is 2 °C and average annual precipitation is 467 mm. Broadleaves were not placed at the boreal site because the litter was not ready before snow made the sites inaccessible. Seven bags of each litter type were collected at each site annually for 4 years. The material remaining in each bag was cleaned of ingrown vegetation and soil, dried at 70 °C and weighed, and used to calculate the average mass of each litter type remaining at each collection time.

ICH experiment

We used three study sites in the moist warm subzone of the Interior Cedar–Hemlock biogeoclimatic zone (ICHmw). At each site was a mature forest and an adjacent clearcut. One site was in the Adams River watershed on the western side of Adams Lake (51°57′N, 119°28′W). The forest at this site was mostly Douglas-fir with some western redcedar and paper birch, about 100 years old. The adjacent 30-ha clearcut was harvested in 1987, broadcast-burned in 1988, and destumped (followed by stump and slash removal) in the fall of 1991. The second site was near Hidden Lake (50°34′N, 118°51′W). The forest at this site was western redcedar, interior Douglas-fir, western larch, and western hemlock, about 140 years old. The adjacent 20 ha was clear-cut in 1978, bunched and burned in 1980, and destumped in the spring of 1992. The third site was near Malakwa (50°58′N, 118°52′W). The 27-ha clearcut adjacent to this site was harvested in 1990 and destumped in the fall of 1991. The Hidden Lake site is in the ICHmw2 subzone in which average annual precipitation is 656 mm and annual mean temperature is 7.5 °C; the Adams Lake and Malakwa sites are in the ICHmw3 subzone in which mean annual temperature is 5.3 °C and average annual precipitation is 671 mm (Lloyd et al. 1990).

Recently abscised leaf litter of western white pine, western redcedar, western larch, Douglas-fir, trembling aspen, and paper birch was collected from forests near the study sites in October 1991. Lodgepole pine needles were collected from a stand in the Kananaskis Valley of Alberta, as part of a province-wide decomposition experiment. Needles were dried at 70 °C and 2 g was placed into bags of fibreglass screening with pore size 1.5 mm. Bags for white pine, birch, and aspen were 15 cm × 15 cm; the others were 10 cm × 10 cm. A double layer of mesh was used to reduce spillage from bags containing Douglas-fir and larch. The average moisture content of broadleaf litter was estimated and 2-g dry mass equivalents were put into bags. There were 180 bags of each species, to allow six collections of five bags of each species from each of the six sites (forest and cutover at three sites). The only exception was Douglas-fir, for which there was not enough litter, so no Douglas-fir samples were collected on the cutover at Adams Lake.

The bags were installed at the six sites on 14–15 November 1991. At 30 locations at each site, one bag of each species was pinned to the ground around a metal stake. All bags were collected from five stations at each site after 0.5, 1, 2, 3, 4, and 5 years. The material remaining in each bag was cleaned of ingrown vegetation and soil, dried at 70 °C and weighed, and used to calculate the average mass of each litter type remaining at each collection time.

Litter chemistry analyses

The analysis procedures and data for the 10 conifer species in the coastal experiment were described in detail by Trofymow et al. (1995). Initial carbon chemistry of these litters was assessed by proximate analysis at Oregon State University. The resulting fractions are nonpolar extractives (NPE; i.e., soluble fats, waxes, and oils), water-soluble extractables (WSE; e.g., simple sugars and water-soluble phenolics), acid-soluble carbohydrates (ACID; i.e., cellulose and hemicellulose), and acid-insoluble residue, commonly referred to as Klason lignin (KLIG) (Preston et al. 1997, 2000).

Litters of the four broadleaf species from the coastal experiment and the seven species from the ICH experiment were analyzed at the B.C. Ministry of Forests research laboratory in Victoria, British Columbia. A Perkin Elmer Series II CHNS/O Analyzer 2400 was used to measure total C and N. Subsamples of the ground foliar litter were digested with Caro's acid using the modification of Parkinson and Allen (1975). Total P was measured using an Alpkem colorimetric autoanalyser, model RFA 300. A Varian Spectra AA400 atomic absorption spectrophotometer was used to measure K, Ca, and Mg. Samples were analyzed for acid detergent cellulose, acid detergent fibre, and acid detergent lignin using the forage fiber analysis procedures (Goering and Van Soest 1970; Ryan et al. 1990).

Concentrations of condensed tannins were determined using the butanol–HCl assay (also known as the proanthocyanidin assay), as described in Preston (1999) and Lorenz et al. (2000). Briefly, samples of 100 mg were extracted twice with 20–22 mL of acetone/water (70/30 by volume); the extracts were combined to make 50 mL; and the extraction residues were dried at 70 °C. Extractable tannins were determined on 1-mL aliquots dried at 70 °C, and on the extraction residues, respectively, and total sample tannin (TAN) expressed as their sum.

The protein-binding capacity of extractable tannins (PTAN) was determined using the radial diffusion assay as described by Hagerman (1987), except that gelatin at 0.5 $mg \cdot mL^{-1}$ was used instead of bovine serine albumin. Aliquots corresponding to approximately 5 $mg \cdot mL^{-1}$ tannin were concentrated by drying at 70 °C, and up to 60 μL was pipetted into each diffusion well. Both assays were standardized using concentration series of purified condensed tannins from balsam fir (*Abies balsamea* (L.) Mill.) tips and salal (*Gaultheria shallon*) foliage (Preston et al. 1997; Lorenz et al. 2000); and the results were expressed as the mean obtained from the two standards.

NMR spectroscopy

Subsamples of litter were finely ground for analysis by standard methods for solid-state ^{13}C NMR with cross-polarization and magic-angle spinning (CPMAS) (Preston 2001). The 10 needle litters used in Experiment 1 were run at 25.18 MHz using a Bruker MSL 100 spectrometer (Bruker Instruments Inc., Karlsruhe, Germany). These NMR spectra and details of the NMR methods were previously reported (Preston et al. 2000). Spectra of the eight litters used

in Experiment 2 were obtained for this study at 75.47 MHz on a Bruker MSL 300 spectrometer, with a zirconium oxide rotor of 7-mm outside diameter, at 4.7-kHz spinning rate, 1-ms contact time, 2-s recycle time, and 6000 scans. In both cases, spectra were processed with 25- to 30-Hz line broadening and baseline correction, and chemical shifts are reported relative to tetramethylsilane (TMS) at 0 ppm, with the reference frequency set using adamantane.

For the coastal experiment, litter spectra were divided into chemical shift regions as follows: 0–50 ppm, alkyl C (abbreviated ALK); 50–60 ppm, methoxyl C (METH); 60–93 ppm, O-alkyl C (OALK); 93–112 ppm, di-O-alkyl and some aromatic C (DIOALK); 112–140 ppm, aromatic C (AROM); 140–165 ppm, phenolic C (PHEN); and 165–190 ppm, carboxyl/carbonyl C (CARBOX). Relative areas of the chemical shift regions for these spectra were determined by cutting and weighing and were expressed as percentages of total area.

For the ICH litters, the relative areas were measured from the integral curves and corrected for intensity in spinning sidebands (SSB), which were larger at the higher magnetic field. The CARBOX region was reduced to 165–185 ppm, and intensities measured for 185–203, 203–223, and 223–245 ppm, corresponding to SSB for AROM, PHEN, and CARBOX regions, respectively. Additional spectra run with dipolar dephasing and total supression of spinning sidebands (DD-TOSS) showed negligible intensity beyond 185 ppm, so that essentially all of the 185–245 ppm region could be attributed to SSB. The relative areas of the AROM, PHEN, and CARBOX regions were then corrected by assuming equal areas of the upfield and downfield sidebands. Several factors can affect the quantitative reliability of cross-polarization (CP) spectra, because of signal loss caused by paramagnetic species and variable CP efficiency, which distorts the relative areas (Preston 2001). However, it is still appropriate to compare intensity distributions among the litter types with similar total C content.

Statistical analyses

In the coastal experiment, the effects of species and sites on percent mass loss over the entire 4-year period were tested by two-way repeated-measures ANOVA. The analysis followed a split-plot design, with time as subplot factor. In the ICH experiment, the effects of species, stand type, and site on percent mass loss over the entire 5-year period were tested by repeated-measures ANOVA. The analysis for the entire 5-year period followed a split-split plot design, with site as block factor, stand type as plot factor, species as subplot factor, and time as sub-subplot factor.

Simple and multiple regression analyses were used to examine relationships between percent mass loss of litter and litter chemistry parameters. Elemental, proximate and NMR variables were tested as predictors of percent mass loss. However, NPE, WSE, and NMR variables were not available for the 4 broadleaves in the coastal experiment, so these variables could only be tested as predictors of mass loss for the 10 conifers. Predictors of mass loss in the coastal experiment were evaluated using 1- and 4-year results, while predictors in the ICH experiment were evaluated using 1- and 5-year results. The rationale was to determine the best one-variable, two-variable, and three-variable regression models for the decomposition experiment at the coastal site and to test the ability of these models to predict percent mass loss for the same litters at the boreal site. Similarly, the best models predicting percent mass loss in the mature stands were tested for their ability to predict percent mass loss of the same litters decomposing in clearcuts.

The coefficient of determination (R^2), residual plots, and regression p values were used to identify the best simple linear regression models. For multiple regressions, candidate models were sought using two or three independent variables. The regression procedure (REG) was used with the adjusted-R-square (ADJRSQ) selection method to identify the top four models with two and three variables, respectively. Models with the fewest possible variables were given preference if all other factors were similar: that is, only two- or three-variable models that improved the degree of explanation were presented.

For the coastal experiment, regression analyses were done for conifers alone (n = 10) and for all species (n = 14, conifers and four broadleaves). Regression models for conifers at the coastal site were subsequently tested with data from the boreal site and compared with the best regression models for percent mass loss at the boreal site.

Regression analyses in the ICH experiment were carried out with data from all seven species decomposing in three forests (n = 21). Regression models were tested on percent mass loss of the same litters in clearcuts and compared with regression models for percent mass loss in clearcuts.

Comparisons of field results and model predictions for percent mass loss of the different litter types were done with absolute values (using Pearson's correlation coefficient) and by rank (using Spearman's correlation coefficient). All statistical analyses were performed using SAS version 6.12 (SAS Institute Inc. 1993).

Results

Coastal experiment

The initial chemistry of the fourteen litter types used in this experiment is described in Tables 1*a* and 1*b*. Among the conifers, N concentrations were highest in hemlock (7.6 mg·g^{-1}) and lowest in larch and amabilis fir (3.9 mg·g^{-1}), and lignin concentrations were highest in cedar (356 mg·g^{-1}) and lowest in spruce (172 mg·g^{-1}). Lignin:N ratios ranged from 29.7 in spruce to 65.8 in cedar, and C:N from 66 in hemlock to 143 in amabilis fir. Except for aspen (5.4 mg·g^{-1}), the broadleaf species had higher N concentrations than did conifers. Alder litter had a higher N concentration (22.0 mg·g^{-1}) than cottonwood (10.2 mg·g^{-1}) and maple (11.7 mg·g^{-1}). Lignin concentrations ranged from 127 mg·g^{-1} in vine maple to 197 mg·g^{-1} in cottonwood. Lignin:N ratios ranged from 8.5 in alder to 34.4 in aspen, and C:N from 23 in alder to 87 in aspen.

Mass loss of needle litter of 10 species over 4 years was significantly faster at the coastal site (Fig. 1*a*) than at the boreal site (Fig. 1*b*). A two-way repeated-measures ANOVA to test effects of site and species on mass loss over the entire 4-year period showed a strong site effect ($P < 0.001$). The effect of species was smaller but significant ($P < 0.01$). The most consistent pattern for the coniferous litters was that cedar decomposed the slowest. At the coastal site, broadleaf

Table 1. Chemistry ($mg \cdot g^{-1}$) of the leaf litters used in the coastal experiment.

(*a*) Initial chemistry of the 10 needle litters and 4 broadleaf litters.

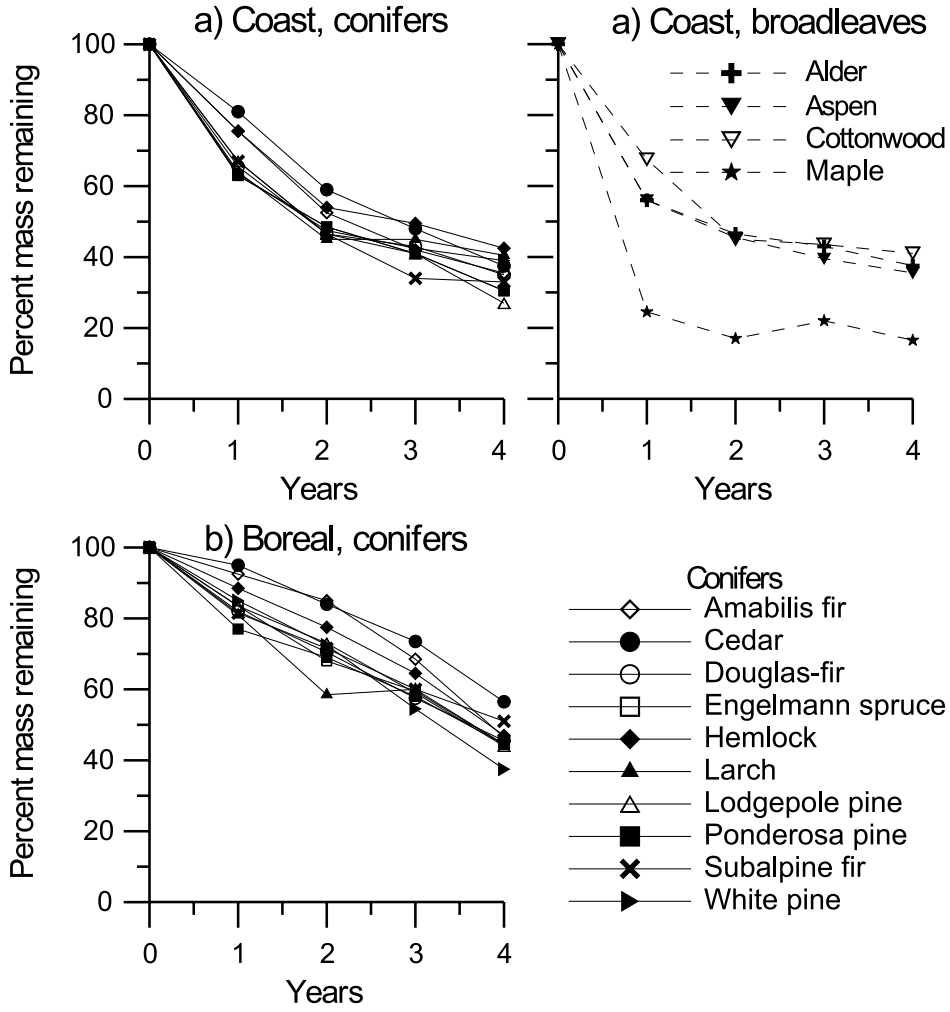
Species	C	N	P	S	K	Ca	Mg	NPE	WSE	ACID	KLIG	Ash	Tannin, total	Tannin, protein-binding	C:N ratio	Lignin:N ratio
Western redcedar	472	5.4	0.51	1.4	0.6	18.9	0.5	107	105	365	356	72.0	27.2	19.3	87.3	65.8
Lodge-pole pine	490	4.7	0.39	2.2	0.5	8.4	1.5	164	259	331	208	41.4	54.3	11.0	104.3	44.2
Western white pine	506	5.5	0.38	1.9	0.8	12.0	1.5	88	315	325	238	35.9	87.7	20.0	92.0	43.3
Ponderosa pine	484	6.0	0.96	1.9	1.7	4.5	1.4	113	266	315	277	30.7	35.8	6.0	80.6	46.2
Western hemlock	503	7.6	0.91	1.5	1.0	7.5	1.1	85	259	290	339	27.8	32.7	0	66.2	44.6
Douglas-fir	477	5.0	0.87	1.9	2.1	22.3	1.1	91	329	317	213	53.4	29.7	0	95.3	42.5
Western larch	457	3.9	2.03	1.6	4.1	4.2	1.3	95	321	325	200	62.3	55.1	0	117.1	51.3
Engelmann spruce	474	5.8	0.64	1.7	2.3	17.4	0.6	132	345	274	172	82.3	13.8	0.9	81.7	29.7
Amabilis fir	559	3.9	0.65	1.7	0.5	12.9	0.5	128	303	282	254	35.6	38.7	21.8	143.3	65.0
Subalpine fir	503	4.4	0.75	2.2	2.4	18.2	1.3	139	340	253	215	56.2	55.6	28.2	114.3	48.8
Red alder	519	22.0	0.60	1.3	2.2	12.5	1.3	nd	nd	300	187	9.7	14.1	50.9	23.6	8.5
Trembling aspen	468	5.4	2.00	0.8	3.5	21.1	3.3	nd	nd	422	186	0	24.0	8.9	86.7	34.4
Black cottonwood	477	10.2	0.80	1.2	14.8	25.5	2.7	nd	nd	433	197	11.2	35.9	8.6	46.8	19.3
Vine maple	473	11.7	1.40	1.5	13.4	19.5	2.9	nd	nd	342	127	7.2	9.4	42.3	40.4	10.9

(*b*) Carbon chemistry of the 10 needle litters.*

Species	Alkyl	Methoxyl	O-alkyl	Di-O-alkyl	Aromatic	Phenolic	Carboxyl
Western redcedar	133.1	10.3	203	54.8	35.2	37.1	23.2
Lodgepole pine	96.6	8.3	224	57.9	51.4	35.2	17.2
Western white pine	75.8	9.4	225	70.6	52.1	54.2	19.4
Ponderosa pine	90.5	12.6	228	57.4	39.7	40.4	15.6
Western hemlock	124.8	9.9	204	57.9	44.9	42.5	19.1
Douglas-fir	98.4	8.6	214	38.7	53.5	37.1	26.6
Western larch	41.9	8.5	230	77.2	37.4	48.6	12.9
Engelmann spruce	154.1	4.9	180	36.2	41.5	35.2	21.7
Amabilis fir	129.0	14.0	222	64.7	52.2	55.2	22.4
Subalpine fir	115.1	5.7	196	56.6	55.8	52.4	21.5

Note: NPE, nonpolar extractives; WSE, water-soluble extractives; ACID, acid-soluble carbohydrates; KLIG, Klason lignin; nd, not determined.
*Values are from total dry litter mass in each spectral region from the nuclear magnetic resonance analyses.

Fig. 1. Mass remaining of foliar litter from (*a*) 14 tree species in a coastal forest and (*b*) 10 tree species in a boreal forest during 4-year incubations.



litters decomposed faster than coniferous litters during the first year or two, but there was little difference among litters other than vine maple by 3 years. Vine maple lost almost 75% of its initial mass during the first year, but mass loss was slow thereafter.

The best six models predicting 1- and 4-year mass loss for the coastal experiment are shown in Tables 2*a* and 2*b*. The two sets of models, one based on the 10 conifer species only and the other on all 14 species, are single and multiple regressions using the initial elemental, proximal and NMR data as variables. The two lower ranking versions of two- and three-variable models were included in Tables 2a and 2*b* only if these models predicted percent mass loss better than models with fewer parameters. For conifers after 1 year, the best one-, two-, and three-variable models all included a negative coefficient for lignin or lignin:N, and alkyl C also contributed with a negative coefficient. For all species after 1 year, the best single variable was lignin, but lignin and lignin:N were not among the variables in the two- and three-variable models.

After 4 years, the best model variables were quite different from those predicting mass loss after 1 year (Table 2*b*). For conifers, none of the models included lignin, lignin:N, or alkyl C. Instead, the best one-, two-, and three-variable models all included a positive coefficient for nonpolar extractives. For all species, the best single variable was lignin, but the relationship was poor.

Among the conifer litters, there was a small range in most litter chemistry variables, which may have limited our ability to determine predictive relationships. Including the broadleaf data broadened the range of most litter chemistry variables. To determine if this improved our predictive ability, we compared the predictive value of the most important litter chemistry variables for conifers with their predictive value when both litter types were included in the data set. This was only possible for lignin, lignin:N, Mg, and S, as the suite of available litter chemistry variables for broadleaves did not include nonpolar extractives and the NMR variables that occurred in the best models for conifers. The inclusion of broadleaves in the data set increased the variation in lignin (vine maple), lignin:N (alder, cottonwood and vine maple), S (alder, aspen, cottonwood), and Mg (aspen, cottonwood, maple). For 1-year mass loss, lignin and lignin:N had higher predictive value ($R^2_{adj.}$) for all species compared to conifers only, but the opposite was the case for Mg (models M2 vs. M1, Table 2*a*). The two-variable model with lignin and Mg (M3-B, Table 2*a*) did not perform better on all species ($R^2_{adj.}$ = 0.57 vs. 0.73). For 4-year mass loss, there was just a slight im-

Table 2. Multiple regression analysis of percent mass loss at the coastal site, using litter chemistry variables.

Source	$R^2_{adj.}$	R^2	B_0	B_1	X_1	B_2	X_2	B_3	X_3	p
(*a*) 1-year percent mass loss.										
One-variable models										
Conifers										
M1	0.45	0.51	49.11	–0.07	KLIG					0.021
M1-B	0.44	0.50	18.83	11.35	MG					0.022
M1-C	0.34	0.41	48.87	–0.37	KLIGN					0.046
All species										
M2	0.49	0.53	71.07	–0.15	KLIG					0.003
M2-B	0.47	0.51	57.57	–0.54	KLIGN					0.004
M2-C	0.40	0.45	20.91	10.19	MG					0.009
Two-variable models										
Conifers										
M3	0.78	0.83	62.12	–0.37	KLIGN	–0.12	ALK			0.002
M3-B	0.73	0.79	35.68	–0.06	KLIG	8.82	MG			0.004
M3-C	0.66	0.74	56.00	–0.06	KLIG	–0.09	ALK			0.009
All species										
M4	0.66	0.71	192.12	0.72	PTAN	–0.34	C			0.001
M4-B	0.59	0.65	79.49	–0.14	KLIG	–0.15	CN			0.003
M4-C	0.57	0.64	18.36	8.44	MG	0.36	PTAN			0.004
Three-variable models										
Conifers										
M5	0.85	0.90	23.90	–0.10	KLIG	0.22	OALK	–0.16	CN	0.002
M5-B	0.82	0.88	50.23	–0.08	KLIG	–0.11	ALK	2.59	N	0.003
M5-C	0.82	0.88	71.73	–0.08	KLIG	–0.10	ALK	–0.11	CN	0.004
All species										
M6	0.70	0.77	142.03	0.60	PTAN	–0.25	C	4.49	MG	0.002
M6-B	0.69	0.76	169.42	0.55	PTAN	–0.26	C	–0.06	KLIG	0.002
(b) 4-year percent mass loss.										
One-variable models										
Conifers										
M1	0.66	0.70	47.18	0.15	NPE*					0.003
M1-B	0.52	0.57	40.51	13.37	S					0.011
M1-C	0.08	0.18	72.88	–0.03	KLIG					0.223
All species										
M2	0.18	0.24	77.37	–0.05	KLIG					0.073
M2-B	0.11	0.18	63.00	0.17	PTAN					0.135
M2-C	0.02	0.09	56.76	5.29	S					0.292
Two-variable models										
Conifers										
M3	0.76	0.81	39.01	0.11	NPE*	7.25	S			0.003
M3-B	0.72	0.78	38.73	17.11	S	–0.12	TAN			0.005
M3-C	0.70	0.77	91.86	–0.72	PHEN	0.51	PTAN			0.006
All species										
M4	0.25	0.37	55.14	10.64	S	–0.19	TAN			0.081
M4-B	0.25	0.36	41.10	10.61	S	4.65	MG			0.084
M4-C	0.25	0.36	68.18	–0.06	KLIG	6.03	S			0.085
Three-variable models										
Conifers										
M5	0.87	0.91	46.82	8.83	S	0.09	NPE*	–0.19	PHEN	0.002
M5-B	0.86	0.91	26.07	0.15	NPE*	0.16	OALK	–0.23	DIOALK	0.002
M5-C	0.83	0.89	38.23	11.36	S	0.08	NPE	–0.08	TAN	0.003

Table 2 (*concluded*).

Source	$R^2_{adj.}$	R^2	B_0	B_1	X_1	B_2	X_2	B_3	X_3	p
All species										
M6	0.66	0.74	36.18	17.98	S	5.54	MG	–0.23	TAN	0.003
M6-B	0.42	0.55	65.03	10.46	S	–0.17	TAN	–0.05	KLIG	0.038
M6-C	0.39	0.53	75.84	0.39	PTAN	–1.25	N	–0.19	TAN	0.047

Note: NPE, nonpolar extractives; KLIG, Klason lignin; KLIGN, lignin:N ratio; PTAN, protein-binding tannins; TAN, total tannins; PHEN, phenolic C; ALK, alkyl C; OALK, O-alkyl C; DIOALK, di-O-alkyl C; S, MG, N, and C are concentrations of sulfur, magnesium, nitrogen, and carbon, respectively; CN, C:N ratio. For conifers, $n = 10$; for all species, $n = 14$.

*NPE variables were only included in regressions for conifers.

provement in the predictive value of lignin when broadleaves were included, but the predictive value of S decreased strongly (models M2 vs. M1, Table 2*b*). The two-variable model with S and tannins (M3-B, Table 2*b*) did not perform better on all species ($R^2_{adj.} = 0.25$ vs. 0.72).

The best three models for conifers at the coastal site (M1, M3, M5) were used to predict percent mass loss at the boreal site after 1 and 4 years. After 1 year, the coastal model predicted percent mass loss at the boreal site fairly well based on Pearson and Spearman correlation analysis on field data and predicted values (Table 3). Although significant, relationships between boreal mass loss and predicted mass loss were less close than between coastal field data and model data. However, after 4 years, the coastal models were not at all able to predict differences in percent mass loss at the boreal site.

The best one-, two-, and three-variable models for predicting percent mass loss at the boreal site after 1 and 4 years were then sought by multiple regression (Table 4*a*). One-year mass loss at the boreal site was best predicted by models with positive coefficients for Mg, K, P, or S, and only the three-variable model also included a negative coefficient for lignin:N. The lower ranking models indicated that lignin and N were also important at the boreal site as at the coastal site, thus explaining the applicability of the coastal models at both sites for 1-year mass loss. As indicated by the small predictive value of the coastal models for 4-year mass loss at the boreal site, a distinctly different set of litter chemistry variables predicted 4-year mass loss at the boreal site (Table 4*b*). All three types of models incorporated a negative coefficient for lignin:N. While phenolic C was included in three-variable models for both sites, O-alkyl C and lignin:N were much better predictors than nonpolar extractives and S at the boreal site, as shown by the close correlations between boreal field data and boreal model predictions (Table 3 and Fig. 2).

Table 3. Pearson's correlation and Spearman's rank correlation coefficients between percent mass loss at the coastal or boreal site vs. percent mass loss predicted by the best three regression models from the two sites (see Tables 2 and 4).

	Pearson's R	p	Spearman's R	p
1–year percent mass loss				
Coastal percent mass loss vs. coastal model prediction				
M1	0.71	0.021	0.37	0.293
M3	0.91	<0.001	0.90	<0.001
M5	0.95	<0.001	0.81	0.005
Boreal percent mass loss vs. coastal model prediction				
M1	0.60	0.068	0.48	0.160
M3	0.82	0.004	0.62	0.056
M5	0.80	0.005	0.61	0.059
Boreal percent mass loss vs. boreal model prediction				
M1	0.68	0.031	0.54	0.111
M3	0.85	0.002	0.90	<0.001
M5	0.94	<0.001	0.92	<0.001
4-year percent mass loss				
Coastal percent mass loss vs. coastal model prediction				
M1	0.84	0.003	0.81	0.004
M3	0.90	<0.001	0.87	0.001
M5	0.96	<0.001	0.96	<0.001
Boreal percent mass loss vs. coastal model prediction				
M1	–0.16	0.667	–0.02	0.960
M3	0.03	0.939	0.10	0.777
M5	–0.01	0.982	0.07	0.855
Boreal percent mass loss vs. boreal model prediction				
M1	0.56	0.090	0.48	0.162
M3	0.87	0.001	0.92	<0.001
M5	0.93	<0.001	0.88	<0.001

ICH experiment

The initial chemistry of the seven foliar litters in this experiment is presented in Tables 5*a* and 5*b*. Concentrations of N were highest in the broadleaves (aspen and birch, about 7 $mg \cdot g^{-1}$) and lowest in cedar (4 $mg \cdot g^{-1}$). Lignin concentrations were lowest in larch (168 $mg \cdot g^{-1}$) and highest in cedar (439 $mg \cdot g^{-1}$). Lignin:N ratios ranged from 30 in birch to 110 in cedar.

The litters lost about 50% of their original mass during the 5-year incubation (Figs. 3*a* and 3*b*). During the first year, aspen lost mass more quickly and white pine more slowly than other litters. After the first year, differences between litters were small and not consistent among the three sites. However, cedar litter tended to decompose most slowly as also noted in the coastal study. The repeated-measures ANOVA showed a highly significant effect of species over the entire 5-year period ($P < 0.001$). Repeated-measures ANOVA also indicated an effect of stand type ($P = 0.077$) with higher mass loss in clearcuts than in forests. There was also a significant species × stand type interaction ($P = 0.001$). The effect of site over the entire 5-year period was not significant ($P = 0.34$).

The relationship between mass loss and litter chemistry variables was analyzed for the litters incubated in forests and clearcuts with 1- and 5-year mass loss values. The best one-, two-, and three-variable models for the forests are shown in

Table 4. Multiple regression analysis of 10 coniferous litters at the boreal site, using litter chemistry variables.

Source	$R^2_{adj.}$	R^2	B_0	B_1	X_1	B_2	X_2	B_3	X_3	p
(*a*) 1-year percent mass loss.										
One-variable models										
M1	0.38	0.45	4.93	9.43	MG					0.035
M1-B	0.34	0.42	30.90	–0.33	KLIGN					0.044
M1-C	0.30	0.38	10.41	2.93	K					0.057
Two-variable models										
M3	0.65	0.72	–11.22	3.07	K	11.90	S			0.011
M3-B	0.61	0.70	2.55	8.07	MG	2.42	K			0.016
M3-C	0.60	0.69	40.33	–0.33	KLIGN	–0.09	ALK			0.017
Three-variable models										
M5	0.82	0.88	0.86	6.56	P	11.83	S	–0.26	KLIGN	0.003
M5-B	0.82	0.88	–30.08	3.69	K	15.35	S	2.21	N	0.004
M5-C	0.82	0.88	–6.03	3.27	K	14.35	S	–0.10	CN	0.004
(*b*) 4-year percent mass loss.										
One-variable models										
M1	0.23	0.32	66.27	–0.26	KLIGN					0.090
M1-B	0.23	0.31	46.12	7.15	MG					0.092
M1-C	0.19	0.28	48.37	0.13	TAN					0.113
Two-variable models										
M3	0.69	0.76	26.27	–0.36	KLIGN	0.21	OALK			0.007
M3-B	0.54	0.64	–0.91	0.08	WSE	0.11	ACID			0.028
M3-C	0.53	0.63	61.15	–0.27	KLIGN	0.13	TAN			0.031
Three-variable models										
M5	0.81	0.87	23.91	–0.41	KLIGN	0.19	OALK	0.23	PHEN	0.005
M5-B	0.73	0.82	9.19	–0.08	KLIG	0.22	OALK	3.38	N	0.012
M5-C	0.72	0.81	26.90	–0.39	KLIGN	0.21	OALK	0.11	PTAN	0.013

Note: KLI, Klason lignin; KLIGN, lignin:N ratio; ALK, alkyl C; TAN, total tannins; PTAN, protein-binding tannins; OALK, O-alkyl C; WSE, water-soluble extractives; ACID, acid-soluble extractives; PHEN, phenolic C; MG, K, S, and N are concentrations of magnesium, potassium, sulfur, and nitrogen, respectively; CN, C:N ratio.

Fig. 2. Observed and predicted mass remaining after 4 years at coastal and boreal sites. HEM, hemlock; WHITE, white pine; AMAB, amabilis fir; DFIR, Douglas-fir; SPRUC, Engelmann spruce; SUBAL, subalpine fire; POND; ponderosa pine; LODGE, lodgepole pine.

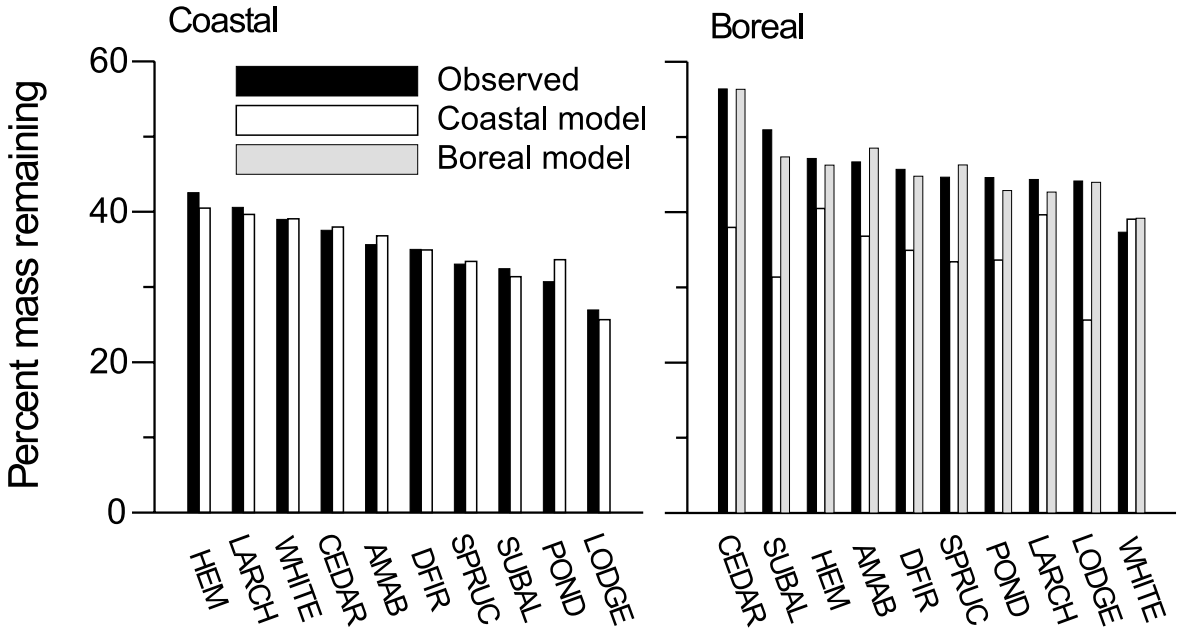


Table 5. Chemistry ($mg \cdot g^{-1}$) of the seven foliar litters used in the Interior Cedar–Hemlock experiment.

(*a*) Initial chemistry.

Species	C	N	P	S	K	Ca	Mg	KLIG	Ash	Cellulose	ACID	Tannin, total	Tannin, protein-binding	C:N ratio	Lignin:N ratio
Lodge pole pine	529	5.3	0.4	0.8	0.16	4.3	1.1	341	15.2	181	536	27.5	8.5	100	64
Western white pine	522	4.5	0.6	0.5	0.11	8.5	1.4	368	23.1	291	682	12.0	0	116	82
Western redcedar	537	4.0	0.4	0.4	0.21	23.1	0.7	439	23.1	479	479	53.1	46.9	134	110
Western larch	511	4.6	1.4	0.4	0.25	4.1	1.0	168	46.9	488	488	33.1	11.7	111	37
Douglas-fir	521	5.2	1.4	0.9	0.27	9.7	0.8	201	37.6	216	455	49.9	9.0	100	39
Trembling aspen	468	7.2	1.1	0.7	0.14	15.6	2.0	330	14.0	223	567	9.9	0	65	46
Paper birch	487	6.9	3.2	0.4	0.97	13.8	3.4	210	11.9	195	417	61.8	22.9	71	30

(*b*) Carbon chemistry.*

Species	Alkyl	Methoxyl	O-alkyl	Di-O-alkyl	Aromatic	Phenolic	Carboxyl
Lodgepole pine	104.2	17.8	228	66.8	50.7	39.3	22.1
Westen white pine	78.0	23.4	218	69.3	67.3	45.4	20.5
Western redcedar	134.6	20.8	201	67.1	49.9	42.4	21.2
Western larch	71.4	18.5	231	73.9	55.4	44.1	17.3
Douglas-fir	110.8	24.3	183	57.9	72.5	47.9	24.7
Trembling aspen	102.9	18.8	171	60.5	46.2	41.0	28.1
Paper birch	88.5	17.5	171	71.0	64.3	49.4	25.3

Note: KLIG, Klason lignin; ACID, acid-soluble carbohydrates.
*Values from total dry litter mass in each spectral region from the nuclear magnetic resonance analyses.

Tables 6*a* and 6*b*. After 1 year, lignin, lignin:N, and alkyl C were not included in the best predictive models. Instead, C or C:P was included with negative coefficients in all three models. After 5 years, the best predicting variables were completely different (Table 6*b*). Calcium was the best single predictor of mass loss, with a negative coefficient, and Ca was also included in two- and three-variable models.These three models were then applied to predict percent mass loss in the clearcuts. Again, predictive models developed in one site type were found to apply in another site type for 1-year mass loss, but not for 5-year mass loss (Table 7, Fig. 4). After 1 year, correlations between clearcut field data and forest model predictions were almost as close as correlations between forest field data and forest model predictions. However, after 5 years the predictors in forests did not work in the clearcuts. For 1-year mass loss of litters in clearcuts (Table 8*a*), the best models included almost the same variables as those that best predicted mass loss in forests (Table 6*a*). For 5-year mass loss the three best models all included a negative coefficient for protein-binding phenolics, while lignin, lignin:N, and alkyl C were not included (Table 8*b*).

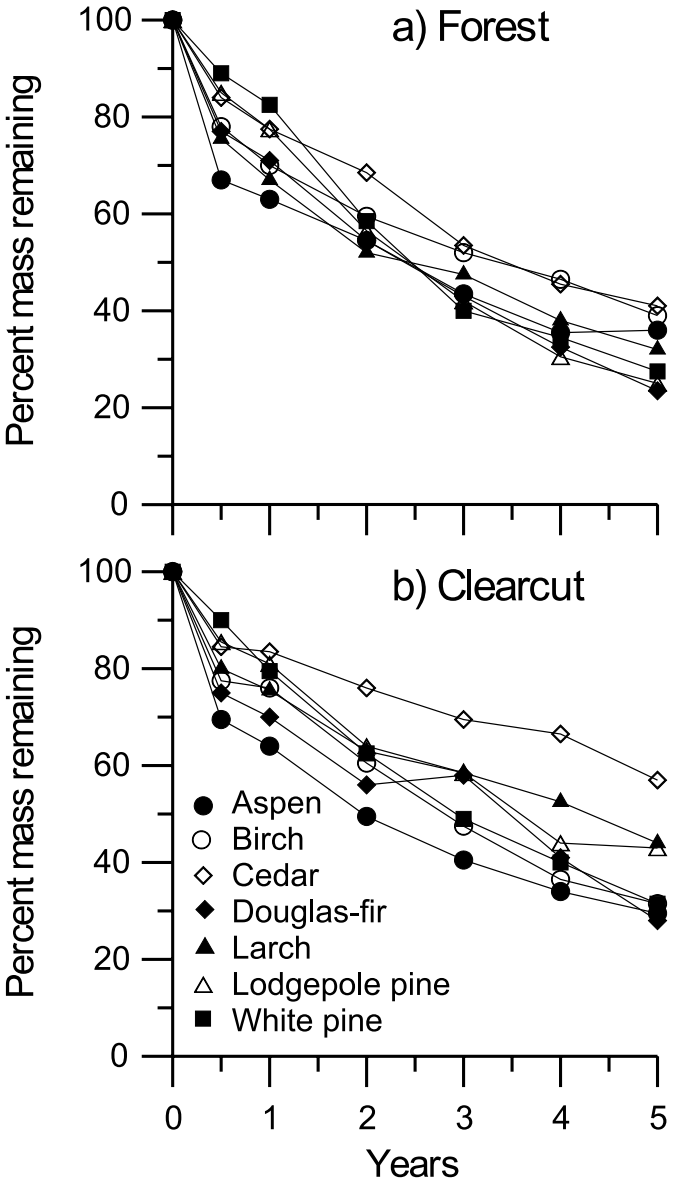
Discussion

Hypothesis 1: broadleaf litters decompose faster than needle litters

The small and fleeting differences between decay rates of broadleaf and needle litter in this study were not in keeping with our hypothesis that broadleaf litter decomposes faster than needle litter. The broadleaf litters decayed faster than needle litters during the first year, but slower in later stages, as has been reported in other studies (Staaf 1980; Cole et al. 1995; Prescott et al. 2000). In the Canadian Intersite Decomposition Experiment (CIDET) study, the order of percent mass loss of aspen, white birch, black spruce, and jack pine litter changed between years 1 (Moore et al. 1999), 3 (Preston et al. 2000), and 6 (Trofymow et al. 2002), also indicating rapid initial but slower later decay of broadleaf litter. This pattern is also consistent with recent reports of broadleaf forests having greater organic matter accumulations (Berg et al. 2001) and less active organic matter (Giardina et al. 2001) than needleleaf forests.

The similar rates of decay may reflect the fairly similar initial chemistries of the needle and broadleaf litters in this study. Vine maple was the only broadleaf that decayed particularly rapidly, and was also the only broadleaf with a particularly low lignin concentration (127 $mg \cdot g^{-1}$). Vine maple is actually an understory tree, often considered a shrub (Pojar and MacKinnon 1994). In the coastal experiment, the broadleaves had higher N (except aspen), higher Ca and Mg, lower lignin, and generally lower tannin concentrations than most of the conifers. In the ICH experiment, the broadleaves had higher N and Mg concentrations, but lignin and tannin concentrations and alkyl and phenolic C contents were similar in broadleaf and needle litters. Thus the common broadleaf overstory trees in British Columbia (alder, aspen, and birch) do not have much better initial chemistries or faster rates of decay than those of the coniferous species.

Fig. 3. Mass remaining of foliar litter from *(a)* seven species in three Interior Cedar–Hemlock forests and (*b*) three clearcuts during 5-year incubations.



Hypothesis 2: relative decomposition rates are predictable from the initial lignin concentration, the lignin:N ratio, or the alkyl-C content of litter

In the coastal experiment, Klason lignin and lignin:N had the highest predictive value, at least in the first year of decay. However, these factors did not correlate with decay rate of litters in the ICH experiment, in which C:P ratios had the highest predictive value. This may be related to the fairly small range of lignin concentrations in foliar litter of British Columbia trees, as discussed above. Expansion of the range of litter used in the coastal experiment to include broadleaf litters improved the predictive value of lignin, and especially lignin:N, for 1-year mass loss. The weak relationship with lignin may also be related to the fairly high concentrations of lignin in these litters. All of the litters except vine maple had lignin concentrations >170 $mg \cdot g^{-1}$, which is near the up-

Table 6. Multiple regression analysis of seven litters incubated in three Interior Cedar–Hemlock forests, using litter chemistry variables.

Source	$R^2_{adj.}$	R^2	B_0	B_1	X_1	B_2	X_2	B_3	X_3	p
(*a*) 1-year percent mass loss.										
One-variable models										
M1	0.45	0.48	136.61	–0.21	C					<0.001
M1-B	0.41	0.44	37.29	–0.17	KLIGN					0.001
M1-C	0.37	0.40	34.18	–0.010	CP					0.002
Two-variable models										
M2	0.68	0.71	63.79	–0.014	CP	–0.46	AROM			<0.001
M2-B	0.63	0.67	102.85	–0.017	CP	–1.44	PHEN			<0.001
M2-D	0.58	0.63	153.20	–0.26	C	0.24	ASH			<0.001
Three-variable models										
M3	0.72	0.77	130.72	–0.020	CP	–2.15	PHEN	0.15	TAN	<0.001
M3-B	0.72	0.76	96.10	–0.021	CP	–1.52	PHEN	0.13	ALK	<0.001
M3-C	0.71	0.75	83.73	–0.014	CP	–0.47	AROM	–0.29	DIOALK	<0.001
(*b*) 5-year percent mass loss.										
One-variable models										
M1	0.41	0.44	77.15	–0.80	CA					<0.001
M1-B	0.33	0.36	54.43	23.30	S					0.004
M1-C	0.28	0.32	72.05	–0.28	PTAN					0.008
Two-variable models										
M2	0.58	0.62	65.30	–0.64	CA	17.11	S			<0.001
M2-B	0.58	0.62	52.28	–0.84	CA	1.25	METH			<0.001
M2-C	0.58	0.62	120.01	–0.93	CA	–0.62	DIOALK			<0.001
Three-variable models										
M3	0.68	0.72	60.72	–1.24	CA	2.60	CARBOX	–7.02	N	<0.001
M3-B	0.67	0.72	150.63	1.31	AROM	–3.45	PHEN	–0.10	KLIGN	<0.001
M3-C	0.66	0.71	89.12	–0.91	CA	0.86	METH	–0.42	DIOALK	<0.001

Note: C, CA, S, and N are concentrations of carbon, calcium, sulfur, and nitrogen, respectively; TAN, total tannins; ALK, alkyl C; PTAN, protein-binding tannins; METH, methoxyl C; DIOALK, di-O-alkyl C; CARBOX, carboxyl C; AROM, aromatic C; PHEN, phenolic C; ASH, ash concentration; CP, C:P ratio; KLIGN, lignin:N ratio.

per end of the relationship between lignin and mass loss, as demonstrated by Taylor et al. (1991) with a broader range of substrates.

No other NMR or proximate variables or pairs of variables had a high predictive value, and many had both positive and negative relationships with mass loss. For example, O-alkyl C is largely due to carbohydrate C, and thus expected to be associated with faster decomposition. It had a positive coefficient, as expected, except for two models for the 5-year data from clearcuts (M2 and M3, Table 8*b*). However, the peak believed to represent O-alkyl C also includes contributions from more resistant cellulose fractions (Huang et al. 1998; Preston et al. 2000), and the sharp signal for C1 of cellulose at 105 may account for the consistently negative influence of the di-O-alkyl region. Conversely, alkyl C is expected to have a negative influence on decay, but had positive coefficients for two models for 1-year ICH sites (M3-B, Table 6*a* and M3-C, Table 8*a*).

Given their protein-binding properties, tannins have been associated with reduced decomposition rate and humus accumulation in nutrient-limited systems (Northup et al. 1998; Preston 1999), but two of the models incorporated positive coefficients for tannins, compared to six with the expected negative coefficient. The protein-binding capacity (PTAN) had a positive coefficient in models for the coastal experiment and a negative coefficient in the ICH experiment.

More consistent results for organic variables were obtained in a similar modelling exercise for 3-year mass loss from the CIDET decomposition experiment (Preston et al. 2000). That study also found a strong negative influence of KLIG (KLIGN was not used), which had much higher predictive value than other proximate or NMR variables. For the NMR variables, ALK and Di-O-ALK were associated with faster decomposition, and METHOX, O-ALKYL, AROM and PHEN had the opposite effect. This discrepancy among study results is probably related to the CIDET study using a broader range of litter types than this study did. Within a litter type (in this case, leaf litter), differences in initial chemistry are small and do not provide for accurate prediction of relative rates of decomposition.

Hypothesis 3: short- (1-year) and long-term (4- to 5-year) mass loss are not predictable from the same litter chemistry variables

In both experiments, the variables best correlated with first-year mass loss were not the same as those best correlated with mass loss after 4 or 5 years. The relationships were also much weaker after 4 or 5 years. This can be attrib-

Fig. 4. Observed and predicted mass remaining after 5 years in the Interior Cedar–Hemlock forest and clearcut sites. WHITE, western white pine; LODGE, lodgepole pine; DFIR, Douglas-fir.

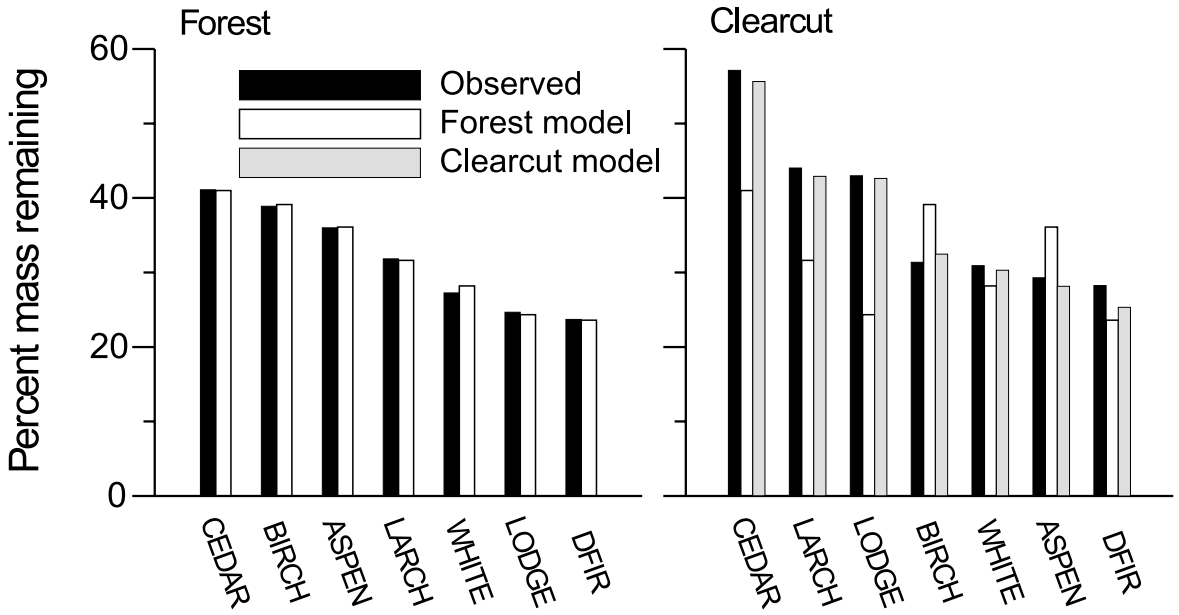


Table 7. Pearson's correlation and Spearman's rank correlation coefficients for percent mass loss of seven litters decomposing in three Interior Cedar–Hemlock forests or three clearcuts vs. percent mass loss predicted by the best three regression models (see Tables 6 and 8).

	Pearson's *R*	*P*	Spearman's *R*	*P*
1-year percent mass loss				
Old-growth percent mass loss vs. old-growth model prediction				
M1	0.69	<0.001	0.79	<0.001
M2	0.84	<0.001	0.88	<0.001
M3	0.87	<0.001	0.88	<0.001
Clearcut percent mass loss vs. old-growth model prediction				
M1	0.78	<0.001	0.82	<0.001
M2	0.73	<0.001	0.69	<0.001
M3	0.73	<0.001	0.72	<0.001
Clearcut percent mass loss vs. clearcut model prediction				
M1	0.78	<0.001	0.82	<0.001
M2	0.88	<0.001	0.76	<0.001
M3	0.94	<0.001	0.88	<0.001
5-year percent mass loss				
Old-growth percent mass loss vs. old-growth model prediction				
M1	0.67	<0.001	0.59	0.005
M2	0.79	<0.001	0.79	<0.001
M3	0.85	<0.001	0.84	<0.001
Clearcut percent mass loss vs. old-growth model prediction				
M1	0.26	0.277	–0.02	0.949
M2	0.36	0.118	0.08	0.736
M3	0.27	0.248	0.26	0.278
Clearcut percent mass loss vs. clearcut model prediction				
M1	0.67	0.001	0.50	0.024
M2	0.83	<0.001	0.79	<0.001
M3	0.88	<0.001	0.79	<0.001

uted to the convergence of decay rates of most litters by 3 years. The small differences among litters in mass loss after 4 or 5 years precludes determination of the factors controlling long-term decay rates by correlation or regression analyses. The lack of relationship between first-year mass loss and long-term mass loss cautions against extrapolating long-term decay rates from short-term (1–2 year) measurements, as is implicit in the derivation of decomposition constants (k values) based on mass loss rates during the first 1 or 2 years. Convergence and even crossing over of mass loss curves of different litters have been reported in long-term studies (Berg and Eckbohm 1991; Prescott et al. 2000; Yang and Janssen 2002), indicating that initial rates of mass loss may not be good indicators of long-term patterns. These findings beg the question: if mass losses of litters are similar after 3 or 4 years, does it matter if some initially decompose faster than others?

Hypothesis 4: the same litter chemistry variables that best predict rates of decay at one site apply to the same litters at other sites

Our comparison of decay of the same litters at different sites indicated that litter chemistry effects on early (first-year) decay were consistent and transferable among sites. Taylor et al. (1991) found that the same factors that predicted rates of decay in forests worked also in a nearby clearcut. The comparisons between sites were not successful with 4- or 5-year mass loss data, probably due to the convergence of mass loss values by this point in decay. Increased interaction between litter type and site-specific conditions may also be expected after 4–5 years, thus masking the consistent litter chemistry effects from the early decay stage.

Implications

The results of these experiments have a number of implications for modelling both the rates of litter decomposition in north temperate forests and the potential effects of climate

Table 8. Multiple regression analysis of seven litters incubated in three Interior Cedar–Hemlock clearcuts, using litter chemistry variables.

Source	$R^2_{adj.}$	R^2	B_0	B_1	X_1	B_2	X_2	B_3	X_3	p
(*a*) 1-year percent mass loss.										
One-variable models										
M1	0.58	0.60	136.31	–0.22	C					<0.001
M1-B	0.	46	0.49	43.64	–0.20	CN				<0.001
M1-C	0.42	0.45	3.54	3.81	N					0.001
Two-variable models										
M2	0.75	0.77	161.61	–0.20	C	–0.55	DIOALK			<0.001
M2-B	0.73	0.76	81.23	–0.010	CP	–0.75	DIOALK			<0.001
M2-C	0.71	0.74	128.15	–0.22	C	13.14	S			<0.001
Three-variable models										
M3	0.87	0.89	119.21	–0.014	CP	–0.63	DIOALK	–0.97	PHEN	<0.001
M3-B	0.87	0.89	303.82	–0.32	C	–1.18	DIOALK	–1.55	CARBOX	<0.001
M3-C	0.85	0.88	20.80	–0.016	CP	–0.25	TAN	0.24	ALK	<0.001
(*b*) 5-year percent mass loss.										
One-variable models										
M1	0.42	0.45	63.84	–0.49	PTAN					0.001
M1-B	0.37	0.40	79.08	–0.06	CELL					0.003
M1-C	0.29	0.33	31.59	5.60	N					0.008
Two-variable models										
M2	0.65	0.68	115.18	–0.52	PTAN	–0.23	OALK			<0.001
M2-B	0.59	0.64	43.75	2.41	CARBOX	–0.37	ALK			<0.001
M2-C	0.56	0.60	180.97	–0.31	C	0.70	AROM			<0.001
Three-variable models										
M3	0.72	0.77	90.60	–0.48	PTAN	–0.21	OALK	0.37	AROM	<0.001
M3-B	0.72	0.77	–8.98	6.08	N	0.81	AROM	–0.25	TAN	<0.001
M3-C	0.71	0.76	9.89	2.62	CARBOX	–0.41	ALK	1.64	METH	<0.001

Note: C, N, S, concentrations of carbon, nitrogen, and sulfur, respectively; CN, C:N ratio; CP, C:P ratio; DIOALK, di-O-alkyl C; PHEN, phenolic C; PTAN, protein-binding tannins; CELL, cellulose; OALK, O-alkyl C; CARBOX, carboxyl C ; ALK, alkyl C; AROM, aromatic C; TAN, total tannins; METH, methoxyl C.

change on those rates. All 14 overstory tree species, including broadleaves, had high initial lignin concentrations and similar rates of decomposition. The small differences in decay rates during the first year disappeared by 3 years. This suggests that long-term litter decay rates may not differ much among forests of different tree species composition in British Columbia (broadleaf, needleleaf, or mixedwood); and, therefore, that changes in tree species composition in response to climatic warming (Ivarson and Prasad 1998; Walther et al. 2002) may not significantly affect rates of foliar litter decay, unless new species with substantially lower lignin concentrations invade these forests

Furthermore, differences in decay rates that would be predicted based on lignin or lignin:N of these litters were not realized in the field study. Thus, at least for the common tree species in British Columbia, models that do not incorporate a litter chemistry influence would actually better represent long-term rates of leaf litter decay in these forests than models that modify rates according to differences in initial litter chemistry.

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