

# Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate

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**Abstract:** The effects of litter quality and climate on decomposition rates of plant tissues were examined using percent mass remaining (MR) data of 10 foliar litter types and 1 wood type during 6 years exposure at 18 upland forest sites across Canada. Litter-quality variables used included initial nutrient contents (N, P, S, K, Ca, Mg) and carbon fractions (determined by proximate analysis and  $^{13}\text{C}$  nuclear magnetic resonance spectroscopy). Climate variables used included mean annual temperature; total, summer, and winter precipitation; and potential evapotranspiration. A single-exponential decay model with intercept was fit using the natural logarithm of 0- to 6-year percent MR data (LNMR) for all 198 type by site combinations. Model fit was good for most sites and types ( $r^2 = 0.64\text{--}0.98$ ), although poorest for cold sites with low-quality materials. Multiple regression of model slope ( $K_f$ ) and intercept ( $A$ ) terms demonstrated the importance of temperature, summer precipitation, and the acid-unhydrolyzable residue to N ratio (AUR/N) ( $r^2 = 0.65$ ) for  $K_f$ , and winter precipitation and several litter-quality variables including AUR/N for  $A$  ( $r^2 = 0.60$ ). Comparison of observed versus predicted LNMR for the best overall combined models were good ( $r^2 = 0.75\text{--}0.80$ ), although showed some bias, likely because of other site- and type-specific factors as predictions using 198 equations accounted for more variance ( $r^2 = 0.95$ ) and showed no bias.

**Résumé :** Les effets de la qualité de la litière et du climat sur les taux de décomposition des tissus végétaux ont été examinés en utilisant les données de pourcentage de masse résiduelle (MR) de 10 types de litière foliaire et un type de bois durant 6 ans d'exposition dans 18 sites forestiers mésiques à travers le Canada. Les variables de qualité de litière utilisées incluent les teneurs initiales en nutriments (N, P, S, K, Ca, Mg) et les fractions carbonées (déterminées par analyse approximative et par spectroscopie à résonance magnétique nucléaire  $^{13}\text{C}$ ). Les variables climatiques utilisées incluent la température annuelle moyenne, les précipitations totale, estivale et hivernale ainsi que le potentiel d'évapotranspiration. Un modèle exponentiel simple de décomposition avec un intercept a été ajusté aux données en utilisant le logarithme naturel des données de pourcentage de MR de 0 à 6 ans (LNMR) pour les 198 combinaisons de sites et de litières. Le modèle s'est bien ajusté pour la majorité des sites et des types de litière ( $r^2 = 0.64\text{--}0.98$ ), bien que plus faiblement pour les sites les plus froids avec des matériaux de faible qualité. La régression multiple de la pente ( $K_f$ ) et de l'intercept ( $A$ ) du modèle a montré l'importance de température, les précipitations estivale et du rapport entre le résidu non hydrolysable à l'acide et N (AUR/N) ( $r^2 = 0.65$ ) dans le cas de  $K_f$  ainsi que de les précipitations hivernale et de plusieurs variables de qualité de litière, incluant AUR/N, dans le cas de  $A$  ( $r^2 = 0.60$ ). Il y avait une relation étroite ( $r^2 = 0.75\text{--}0.80$ ) entre les valeurs observées et prédites de LNMR pour les meilleurs modèles combinés malgré certains

Received 23 January 2001. Accepted 15 June 2001. Published on the NRC Research Press Web site at <http://cjf.nrc.ca> on 26 April 2002.

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biais probablement dus à d'autres facteurs spécifiques au site ou au type de litière étant donné que les prédictions utilisant les 198 équations comptaient pour la majeure partie de la variance ( $r^2 = 0,95$ ) et ne montraient aucun biais.

[Traduit par la Rédaction]

## Introduction

Northern boreal and temperate forests contain large stores of organic carbon (C) in litter, soils, and peats that are estimated to be in the range of 800–900 Pg C (Apps et al. 1993; Schlesinger 1997), and inputs to and decomposition from these stores play a large role in the terrestrial global C cycle (Schimel 1995). These stores could be especially significant if the release of C is accelerated as the result of global warming (Jenkinson et al. 1991), which is predicted to be especially large for midcontinental, high-latitude regions (Houghton et al. 1994). This accumulated C is largely the result of restricted decomposition rates. Three major causes for these restrictions include climate (temperature and moisture), substrate quality (chemical and physical characteristics), and the composition and abundance of the soil biotic communities (Berg 2000; Prescott et al. 2000).

The influence of climate and substrate quality on fresh litter decomposition has been well documented (e.g., Aber et al. 1990; Aerts 1997; Berg et al. 1993; Coûteaux et al. 1995; Meentemeyer 1978; Melillo et al. 1982; Taylor et al. 1991). However, the findings to date are limited by the range of ecological sites, number of tissue types, and length of study. The latter limitation is particularly important as understanding the factors controlling later stages of decomposition are needed to determine the potential fate of the organic matter stores with climate change. In particular, the role of temperature on the decomposition of well-decayed organic matter has been the subject of some debate (Grace and Rayment 2000). In an analysis of literature, Giardina and Ryan (2000) concluded that decomposition rates of well-decayed soil organic matter are not strongly controlled by temperature and that increased temperature alone would not stimulate decomposition of forest-derived C in mineral soil.

More recently, several studies have begun to examine decomposition processes over a much broader range of site, climate, and litter qualities including the Long-Term Intersite Decomposition Experiment in the United States (LIDET 1995), the Decomposition Study (DECO) in Europe (Berg et al. 1993), and the Canadian Intersite Decomposition Experiment (CIDET) in Canada (Trofymow et al. 1995; Trofymow and CIDET Working Group 1998). One of the main goals of these studies is to determine the nature of the controls on litter decay by examining decomposition over many years (usually 10 years or more). When completed these studies will provide critical information on factors controlling later stages of decomposition. Such data are needed to improve national models of C balance (Kurz et al. 1992; Kurz and Apps 1999).

In this paper we present the results from CIDET describing the decomposition of a range of litter types (tree leaves, needles, herbs, and wood) over 6 years at forested sites ranging from the transitional grassland to the subarctic. We have already reported how, across all sites and types, mass remaining after 3 years (Moore et al. 1999) and 1 and 3 years

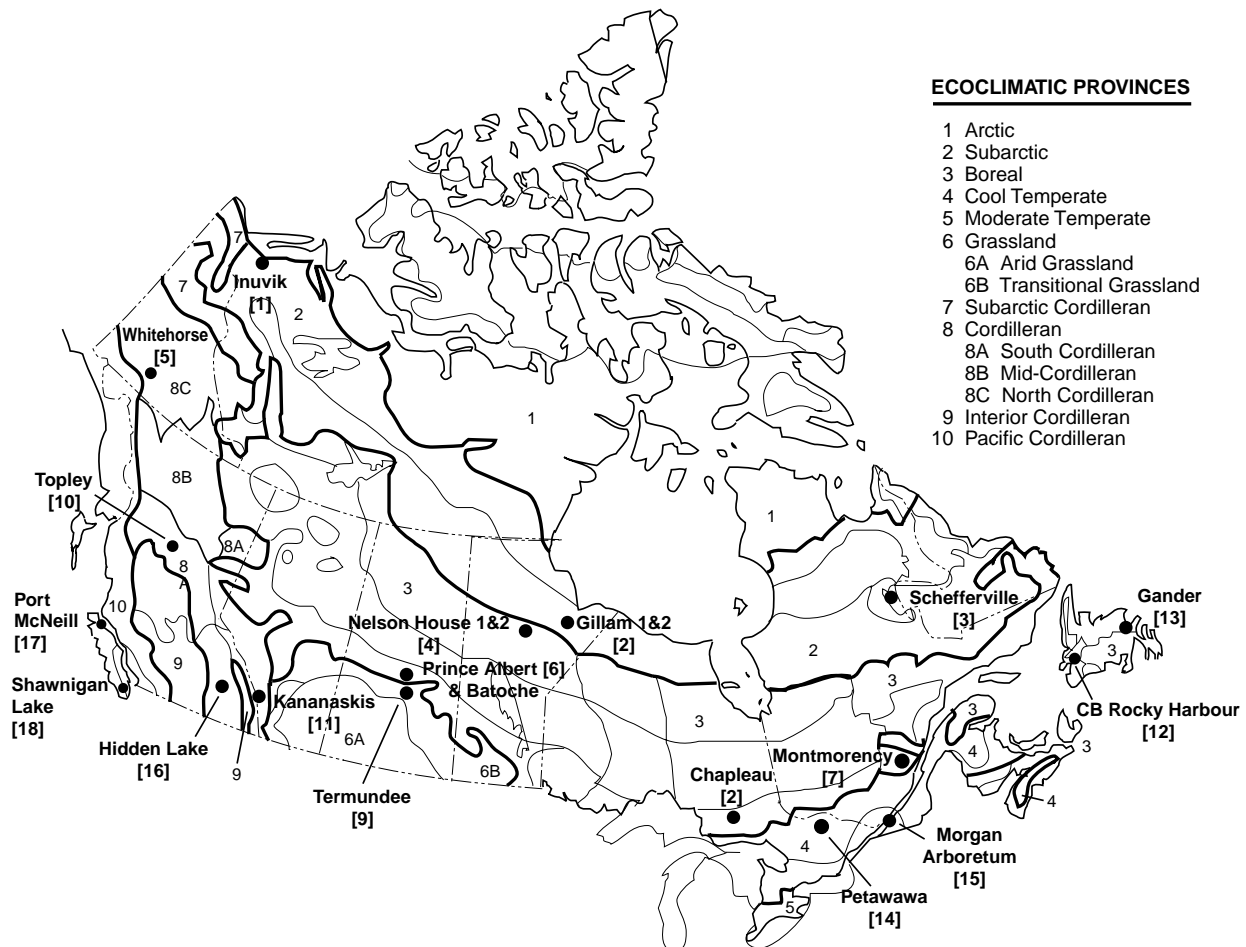
(Preston et al. 2000) was related to mean annual temperature, annual precipitation, and the acid-unhydrolyzable residue (Klason lignin) to N ratio. In this paper we examine how mass remaining at 6 years is related to an expanded set of climate and litter-quality variables. We test the utility of the exponential decay model to describe the mass loss over the 6 years and relate the slope and intercept values of the exponential regression to the same climate and litter-quality variables.

## Methods

The CIDET study was established in autumn 1992, with placement of about 11 000 litterbags containing 11 material types (10 foliar litters, surface and buried wood blocks) at 21 locations (18 upland, 3 wetland sites), representing the major ecoclimatic provinces of Canada (Ecoregions Working Group 1989) (Fig. 1). Details on litter collection, field methods, sample processing, and site descriptions have been published previously (Trofymow and CIDET Working Group 1998; also available as a PDF file at <http://www.pfc.cfs.nrcan.gc.ca/climate/cidet>). The 18 upland sites (3 wetland sites excluded) and 11 material types (buried blocks excluded) examined in this paper are listed in Tables 1 and 2.

The 10 standard foliar litter types were collected from litter traps or senescent tissues. Each litter type was collected from single location and distributed to all sites. Wood blocks were cut from heartwood of a single western hemlock (*Tsuga heterophylla*) log avoiding branch knots. Litters were air-dried, thoroughly mixed, and subsampled to determine air-dry to oven-dry conversion. Subsamples were thoroughly milled to pass a 0.2-mm mesh prior to chemical characterization, which included total elemental analysis (C, N, P, S, Ca, Mg, K) and analysis of C fractions by wet chemical proximate analysis and  $^{13}\text{C}$  nuclear magnetic resonance spectroscopy with cross-polarization and magic-angle spinning (CPMAS NMR). All data were expressed on a milligrams per gram oven-dry substrate basis. The proximate fractions were (i) nonpolar extractables (NPE, soluble fats, waxes and oils), (ii) water-soluble extractables (WSE, simple sugars, soluble phenolics), (iii) acid-hydrolyzable fraction (AHF, primarily cellulose and hemicelluloses), (iv) acid unhydrolyzable residue (AUR, organic portion of residue, i.e., corrected for ash), and (v) ash (ASH). The final residue left after acid hydrolysis during proximate analysis contains a mixture of mineral and organic materials, and ash content must be determined to calculate the organic portion of the residue. Furthermore, the organic residue is not a single chemical compound such as lignin. Preston et al. (1997) demonstrated through NMR analysis that the organic residue prepared from proximate analysis of a variety of litter types contains a mixture of organic compounds including lignin and that condensed tannins and waxes make up from 40 to 60% of the organic residue. In this paper we use the term

**Fig. 1.** Locations of the 18 upland forest sites and their distributions within the ecoclimatic provinces of Canada (Ecoregions Working Group 1989). The three wetland sites (Batoche, Nelson House 2, Gillam 2) were excluded from the analysis in this paper.



AUR to refer to the organic residue left after proximate chemical analysis, i.e., residue corrected for ash content.

The NMR spectra were divided into chemical shift regions as follows: (i) 0–50 ppm, (alkyl C), (ii) 50–60 ppm (methoxyl C), (iii) 60–93 ppm (*O*-alkyl C), (iv) 93–112 ppm (di-*O*-alkyl and some aromatic C), (v) 112–140 ppm (aromatic C), (vi) 140–165 ppm (PHEN, phenolic C), and (vii) 165–190 ppm (CARB, carboxyl or carbonyl C).

Descriptions of the procedures (Trofymow and CIDET Working Group 1998) and results for the elemental and proximate analyses (Trofymow et al. 1995) and  $^{13}\text{C}$  CPMAS NMR analysis (Preston et al. 1997, 2000) have been previously published.

Litterbags were made of 20 × 20 cm polypropylene fabric with 0.25 × 0.5 mm openings. Bags contained 10 g of litter or 50-g wood blocks. Each litter type was placed at all sites, in four replicate plots per site. Bags were placed so they were in contact with the forest floor, where present, thick standing grass or lichen layers were moved aside. Sufficient bags were placed to allow for 10 annual collections. After collection, litterbags were oven-dried at 55°C, the litter remaining weighed and percent mass remaining calculated. In this paper we use 6 years of decomposition data collected for the 10 foliar litters and the surface wood blocks (11 material types) (Table 2) for the 18 upland forest sites (Table 1).

Mean monthly and annual climatic data for the 18 sites were obtained for the closest corresponding long-term Environment Canada meteorological station (Trofymow and CIDET Working Group 1998). Climatic data for both 30-year normals (1951–1980) (Environment Canada 1982a, 1982b) and the 6-year study period (1992–1998) (Environment Canada 2000) were used, although preliminary analysis showed the 30-year normals and 6-year actual climatic data were highly correlated (annual temperature,  $r^2 = 0.9799$ ; annual precipitation,  $r^2 = 0.9936$ ). Potential evapotranspiration (Thorntwaite and Mather 1957) for each of the 18 sites came from values calculated from station climatic data (Agriculture and Agri-food Canada 1997). Climatic variables used in the analyses included (i) mean annual temperature 1951–1980 (T30) or 1992–1998 (T6), (ii) mean total annual precipitation 1951–1980 (P30) or 1992–1998 (P6), (iii) mean summer precipitation July–August 1951–1980 (SP30) or 1992–1998 (SP6), (iv) mean winter precipitation October–March 1951–1980 (WP30) or 1992–1998 (WP6), and (v) precipitation minus potential evapotranspiration 1961–1990 (PPET30).

Relationships between the 9 climatic and 19 litter-quality variables and the mass remaining or exponential decay model parameters were determined using stepwise multiple regression (REG procedure with RSQUARE option; SAS Institute Inc. 1989). For each collection year, the means of the

**Table 1.** Remaining litter mass, averaged across all 11 litter types, at 18 upland sites after 6 years.

Site No.	Location	Mass remaining (%)	T30 <sup>a</sup> (°C)	P30 <sup>b</sup> (mm)	Latitude (N)	Longitude (W)
1	Inuvik, N.W.T.	79 (4.0)	-9.8	266	68°19'	133°32'
5	Whitehorse, Y.T.	72 (4.3)	-1.2	261	60°51'	135°12'
2	Gillam1, Man., upland	65 (4.8)	-5.2	485	56°19'	94°51'
6	Prince Albert, Sask., upland	60 (5.3)	0.1	398	45°55'	77°35'
4	Nelson House1, Man., upland	59 (4.2)	-3.9	542	55°55'	98°37'
3	Schefferville, Que.	53 (5.2)	-4.8	769	54°52'	66°39'
9	Termundee, Sask.	49 (3.9)	1.8	371	51°50'	104°55'
11	Kananaskis, Alta.	45 (3.9)	2.8	657	51°00'	115°00'
10	Topley, B.C.	42 (5.0)	2.5	513	54°36'	126°18'
13	Gander, Nfld.	38 (3.2)	4.3	1130	48°55'	54°34'
7	Montmorency, Que.	37 (3.3)	0.6	1494	47°19'	71°08'
12	Rocky Harbour, Nfld.	36 (4.6)	4.2	1200	49°32'	57°50'
16	Hidden Lake, B.C.	35 (4.1)	6.3	547	50°33'	118°50'
17	Port McNeill, B.C.	35 (4.1)	7.9	1783	53°13'	105°58'
8	Chapleau, Ont.	30 (1.7)	1.1	834	47°38'	83°14'
14	Petawawa, Ont.	29 (1.7)	4.3	822	50°36'	127°20'
18	Shawnigan Lake, B.C.	28 (2.6)	9.3	1215	48°38'	123°42'
15	Morgan Arboretum, Que.	24 (2.3)	6.1	863	45°25'	73°57'
	All	45 (1.4)				

**Note:** Values in parentheses is the standard error of the mean for all litter types at a site. Sites are ordered from low to high values of percent mass remaining.

<sup>a</sup>Mean annual temperature 1951–1980.

<sup>b</sup>Mean annual total precipitation 1951–1980.

**Table 2.** Remaining litter mass, averaged across all 18 sites, for each of the 11 litter types after 6 years; acid-unhydrolyzable residue (AUR) concentration, nitrogen (N) concentration; and AUR/N ratio.

Type code	Species	Mass remaining (%)	AUR (mg/g)	N (mg/g)	AUR/N
Whw	Western hemlock ( <i>Tsuga heterophylla</i> (Raf.) Sarg.) wood blocks	72 (5.1)	294	1.9	154.7
Ctp	Western redcedar ( <i>Thuja plicata</i> Donn ex D. Don) needles	53 (4.7)	356	6.4	55.5
Dbf	Beech ( <i>Fagus grandifolia</i> Ehrh.) leaves	51 (4.2)	280	7.1	39.4
Clf	Tamarack ( <i>Larix laricina</i> (Du Roi) K. Koch) needles	48 (4.3)	262	5.9	40.6
Cdc	Douglas-fir ( <i>Pseudotsuga menziesii</i> (Mirb.) Franco) needles	46 (4.5)	303	7	43.3
Fbf	Bracken fern ( <i>Pteridium aquilinum</i> (L.) Kuhn)	44 (3.8)	329	8.8	37.4
Cpj	Jack pine ( <i>Pinus banksiana</i> Lamb.) needles	42 (4.2)	328	12.8	25.6
Dpt	Aspen leaves ( <i>Populus tremuloides</i> Michx.)	42 (3.4)	144	6.7	21.4
Csb	Black spruce ( <i>Picea mariana</i> (Mill.) BSP) needles	36 (4.0)	283	7.3	38.7
Dbw	White birch ( <i>Betula papyrifera</i> Marsh.) leaves	34 (3.9)	240	7.2	33.3
Gfh	Fescue grass ( <i>Festuca hallii</i> (Vasey) Piper)	32 (1.8)	112	7.1	15.7

**Note:** Values for mass remaining are means with SEs given in parentheses. Litter types are ordered from high to low values of percent mass remaining.

replicates for each material type within a site ( $n = 4$ ) were used for all analyses ( $n = 198$ , 11 materials  $\times$  18 sites). Since wood differs greatly from foliar litters in its chemical properties, some analyses were repeated with wood excluded ( $n = 180$ ). The best of the multiple-variable models were selected on the basis of the  $r^2$  fit.

## Results and discussion

### Mass remaining after 6 years

Six year mass loss averaged 55% (i.e., 45% mass remain-

ing) across all sites and litter types. The highest mass loss was found at the most southerly sites (e.g., Morgan Arboretum, 24% mass remaining; Shawnigan Lake, 28%) and the least at the most northerly sites (e.g., Inuvik, 79% mass remaining; Whitehorse, 72%) (Table 1). Within foliar litters, fescue (*Festuca hallii*) decayed the most rapidly (32% mass remaining), and western redcedar (*Thuja plicata*) the least (53% mass remaining) (Table 2). Wood decayed the least of all material types (72% mass remaining). Variation in mass remaining was lowest for sites and litter types with the greatest mass loss (e.g., Shawnigan Lake, SE = 1.5; fescue,

SE = 1.8) and highest for sites and types with least mass loss (e.g., Inuvik, SE = 4.0; wood, SE = 5.1) (Tables 1 and 2).

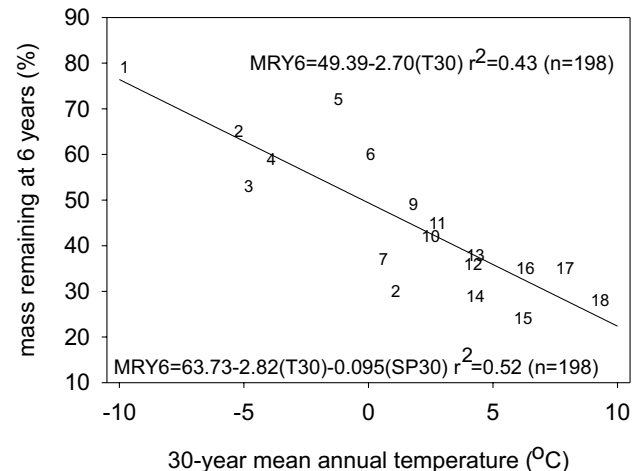
### Climatic and litter-quality controls

Much of the variation in mass remaining amongst sites can be explained by differences in climate. The 18 sites cover a broad range of conditions from the mild (9.3°C) and wet (1783 mm) Pacific cordilleran ecoclimatic region (Shawnigan Lake, Port McNeill) to the cold (−9.8°C) and dry (266 mm) subarctic (Inuvik) with most differences amongst sites due to mean annual temperature. Moore et al. (1999) found that across all litter types mean annual temperature was the best single climate predictor of mass remaining. This was also the case at 6 years ( $r^2 = 0.433$ ,  $n = 198$ ) (Fig. 2) with either the 30-year normal (T30) or 6-year actual (T6) mean annual temperature predicting mass remaining equally well (Table 3). Inclusion of summer precipitation (SP) in a two-variable model improved the fit ( $r^2 = 0.511$ ), and again, T30 and T6 predicted mass remaining similarly (Table 3). Inclusion of PPET improved the overall fit slightly ( $r^2 = 0.512$ ) but not sufficiently to warrant the use of a three-variable model. The analysis was repeated with wood excluded (Table 3A), and  $r^2$  increased by 5–10% with the same set of climate variables, although there were slight changes in parameter values. The best three-variable model included actual annual temperature (T6) and summer precipitation (SP6), but  $r^2$  was only 1% greater than that obtained using the 30-year normals. As the PPET data was only available as 30-year normals, and to reduce the total number of variables used, only 30-year climate normal variables were used for all subsequent analyses.

Variation in mass remaining (MR) amongst material types can be explained by differences in quality. The different materials covered a broad range of N and AUR concentrations, with wood greatly different from the foliar litter types (Table 2). Previous studies (Melillo et al. 1982, 1989; Taylor et al. 1989, 1991) and the 3-year results of this study (Moore et al. 1999; Preston et al. 2000) found that ratio of the acid-unhydrolyzable residue to nitrogen (AUR/N) was the best single litter-quality predictor of litter decomposition. This was also true for the 6-year data; of all litter-quality measures, AUR/N gave the best fit ( $r^2 = 0.22$ ) when wood was included in the regression (Fig. 3, Table 3B). The fit was poor ( $r^2 = 0.07$ ) when wood was excluded (Fig. 3, Table 3). Thus, wood appears as an outlier compared with the other foliar litters, and the relationship between mass remaining and AUR/N with wood included is not linear. For this reason, subsequent analyses were done twice, with wood included or excluded from the data. Similar findings were made by Taylor et al. (1991) who examined decay of materials with a wide range of AUR (Klason lignin) values and found that a piecewise linear model gave the best fit. Additional litter-quality variables slightly improved fits with  $r^2$  increasing by 2–3%, not enough to warrant their inclusion (Table 3). As Preston et al. (2000) found for the 3-year results, variables entering the two- and three-variable models differed if wood was included or not. The  $^{13}\text{C}$ -NMR measurements of CARB and PHEN entered for data including wood, and carboxylics, Ca, and P entering for data with foliar litters alone (Table 3).

For the combination of litter quality and climate the best two-variable regression with wood in the data set included

**Fig. 2.** Relationship between percent mass remaining after 6 years and mean annual temperature (T30) among the 18 upland forest sites; site numbers are as in Table 1. Although only mean values for each site are plotted, regression equations were developed using data for all types and sites (Table 3). The addition of summer precipitation (SP30) significantly increases the  $r^2$ .



the variables AUR/N and T30 ( $r^2 = 0.66$ ,  $p < 0.001$ ) (Table 3). Summer precipitation (SP30) entered as the best third variable, increasing  $r^2$  by 8% ( $r^2 = 0.74$ ). The best fourth and fifth variables were  $^{13}\text{C}$ -NMR measures of litter quality (CARB or PHEN), but they increased the  $r^2$  by less than 2%. With wood excluded, T30 and SP30 were the best two variables ( $r^2 = 0.65$ ). AUR/N entered as the best third variable, increasing  $r^2$  by 7% ( $r^2 = 0.72$ ). The fourth and fifth variables entering were a variety of litter-quality variables (CARB, PHEN, ASH) each adding less than 3% to the  $r^2$  (Table 3). These results are similar to those found by Moore et al. (1999) for the 3-year data, except that SP30 was a better precipitation variable for the 6-year data than P30. The SP30 values were not used in the analysis of the 3-year data. Summer precipitation might be a preferred variable, as it would be a better predictor of sites where surface moisture might be a limiting factor during warmer periods of the year.

### Changes in controls of litter decomposition over time

Since new variables were added for the 6-year analysis as compared with those used for the 3-year (Moore et al. 1999) and 1- and 3-year (Preston et al. 2000) analyses, the data for years 1 and 3 were reanalyzed by stepwise multiple regression to test for the importance of the additional variables. The three best variables and parameter values for predicting percent mass remaining changed from years 1–3 to 6 (Table 4). In year 1 the best variables included two litter-quality variables that differed if wood was included (AUR, AUR/N) or excluded (PHEN, WSE) from the data, and one climate variable (WP30). These were the same litter-quality variables found by Preston et al. (2000) in the analysis of the year-1 data.

Variables in year 1 differed considerably from those for years 3 and 6, which included a temperature (T30) and precipitation (P30 or SP30) variable and one litter-quality variable (AUR/N). The strong influence of litter quality and winter precipitation in year 1 suggests that the important factors controlling mass loss in the first year might be re-

**Table 3.** Multiple regression results of best one- to three-variable models for percent mass remaining at year 6 (MRY6) for data including (with, W) wood ( $n = 198$ ) or excluding (no, N) wood ( $n = 180$ ) and using climate, litter quality, or all climate and litter quality variables.

Regression model	$r^2$	Intercept		Variables and parameter estimates									
		$\Delta r^2$	$B_0$	$B_1$	$X_1$	$B_2$	$X_2$	$B_3$	$X_3$	$B_4$	$X_4$	$B_5$	$X_5$
Climate													
With wood													
MRY6-Wa1	0.389		51.51	-2.8054	T6								
MRY6-Wa1a	0.433		49.39	-2.7021	T30								
MRY6-Wa2	0.511	0.08	61.97	-2.7948	T30	-0.0865	SP30						
MRY6-Wa2a	0.517	0.08	63.73	-2.8200	T30	-0.0953	SP6						
MRY6-Wa3	0.512	0.00	62.61	-2.8957	T30	-0.0945	SP30	0.0023	PPET30				
MRY6-Wa3a	0.523	0.01	72.19	-3.3580	T6	-0.1387	SP6	0.0040	PPET30				
No wood													
MRY6-Na1	0.479		48.74	-2.7681	T6								
MRY6-Na1a	0.538		46.66	-2.6757	T30								
MRY6-Na2	0.639	0.10	59.46	-2.7700	T30	-0.0880	SP30						
MRY6-Na2a	0.650	0.11	61.41	-2.7969	T30	-0.0980	SP6						
MRY6-Na3	0.640	0.00	59.86	-2.8332	T30	-0.0930	SP30	0.0015	PPET30				
MRY6-Na3a	0.655	0.00	69.47	-3.2923	T6	-0.1381	SP6	0.0033	PPET30				
Litter quality													
With wood													
MRY6-Wb1	0.224		33.35	0.2622	AUR/N								
MRY6-Wb2	0.244	0.02	18.86	0.5520	CARB	0.3323	AUR/N						
MRY6-Wb3	0.263	0.02	-9.81	0.8685	CARB	0.3546	DIOAL	0.3768	AUR/N				
No wood													
MRY6-Nb1	0.072		27.57	0.4318	AUR/N								
MRY6-Nb2	0.103	0.03	33.92	0.5730	PHEN	-0.0475	WSE						
MRY6-Nb3	0.129	0.03	20.99	1.6092	CARB	0.4345	CA	-27.8467	P				
Climate and litter quality													
With wood													
MRY6-Wc1	0.433		49.39	-2.7021	T30								
MRY6-Wc2	0.657	0.22	37.33	0.2622	AUR/N	-2.7021	T30						
MRY6-Wc3	0.735	0.08	49.91	0.2622	AUR/N	-2.7948	T30	-0.0865	SP30				
MRY6-Wc4	0.755	0.02	35.42	0.5520	CARB	0.3323	AUR/N	-2.7948	T30	-0.0865	SP30		
MRY6-Wc5	0.764	0.01	46.37	0.3948	PHEN	-0.0340	WSE	0.2035	AUR/N	-2.7948	T30	-0.0865	SP30
No wood													
MRY6-Nc1	0.538		46.66	-2.6757	T30								
MRY6-Nc2	0.639	0.10	59.46	-2.7700	T30	-0.0880	SP30						
MRY6-Nc3	0.711	0.07	44.30	0.4318	AUR/N	-2.7700	T30	-0.0880	SP30				
MRY6-Nc4	0.743	0.03	50.65	0.5730	PHEN	-0.0475	WSE	-2.7700	T30	-0.0880	SP30		
MRY6-Nc5	0.730	0.02	34.61	0.4844	CARB	0.4045	AUR/N	-2.7700	T30	-0.0880	SP30		
MRY6-Nc6	0.759	0.03	18.80	0.3281	PHEN	0.2154	ASH	0.0651	AUR	-2.7700	T30	-0.0880	SP30

**Note:** Within each group of models the  $\Delta r^2$  is the incremental change in  $r^2$  from a model with one less variable ( $X_i - 1$ ). ASH, ash; AUR, acid-unhydrolyzable residue; AUR/N, acid-unhydrolyzable residue/nitrogen ratio; CA, calcium; CARB, carboxyl and carbonyl carbon; DIOAL, di-O-alkyl and some aromatic carbon; PHEN, phenolic carbon; PPET30, precipitation minus potential evapotranspiration 1961–1990; SP6, 6-year mean summer precipitation (July–August, 1992–1998); SP30, 30-year mean summer precipitation (July–August, 1951–1980); T6, 6-year mean annual temperature (1992–1998); T30, 30-year mean annual temperature (1951–1980); WSE, water-soluble extractables.

**Table 4.** Comparisons of best three-variable regression models for percent mass remaining at year 1 (MRY1), year 3 (MRY3), and year 6 (MRY6) for data including (with, W) wood ( $n = 198$ ) or excluding (no, N) wood ( $n = 180$ ) and using all climate and litter quality variables.

Regression model	$r^2$	Intercept ( $B_0$ )	Variables and parameter values					
			$B_1$	$X_1$	$B_2$	$X_2$	$B_3$	$X_3$
<b>With wood</b>								
MRY1-W3	0.754	56.24	0.0726	AUR	0.1748	AUR/N	−0.0185	WP30
MRY3-W3	0.713	63.53	0.2854	AUR/N	−1.6006	T30	−0.0154	P30
MRY6-W3	0.735	49.91	0.2622	AUR/N	−2.7948	T30	−0.0865	SP30
<b>No wood</b>								
MRY1-N3	0.763	70.90	0.7772	PHEN	−0.0679	WSE	−0.0203	WP30
MRY3-N3	0.738	50.87	0.6926	AUR/N	−1.5882	T30	−0.0170	P30
MRY6-N3	0.711	44.30	0.4318	AUR/N	−2.7700	T30	−0.0880	SP30

**Note:** Variables are as defined in Table 3. P30, 30-year mean annual precipitation (1951–1980); WP30, 30-year mean winter precipitation (October–March, 1951–1980).

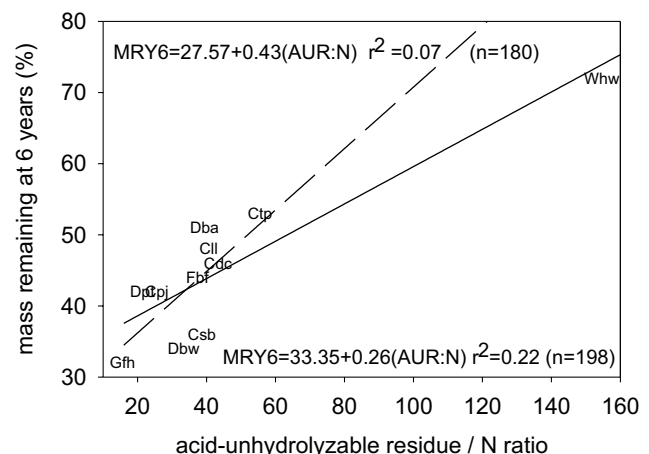
lated to the loss of soluble compounds including soluble carbohydrates, phenolics, and tannins. Soluble carbohydrates would be easily decomposed, and once soluble phenolic compounds were leached, decomposition of the remaining litter could proceed more rapidly than for those litter types with a greater fraction of insoluble phenolic compounds. Since litterbags at all sites were placed in the field in autumn the amount of leaching would be related to the amount of winter rain or the amount of snow and, hence, snowmelt in the spring. Sites with the greatest winter precipitation (over 600 mm from October to March) were maritime sites in coastal British Columbia (Port McNeill and Shawnigan Lake) and the wet east-coast boreal forests (Montmorency, Rocky Harbour, and Gander). Certainly, decomposition in the winter cannot be discounted as temperatures under the snow can be well above air temperatures such that significant mass loss can occur during the winter even in the sub-arctic (Moore 1983).

These findings have implications for generalized decomposition models as few published models include leaching losses. Of the four models (CENTURY, DOCMOD, MBLGEN, GENDEC) used by Moorhead et al. (1999) to examine 2-year mass loss of selected litters and sites from LIDET, only DOCMOD (Currie and Aber 1997) includes losses due to leaching. Even in DOCMOD the process of leaching is not explicitly modelled. Litter is partitioned into three chemical pools, lignin-bound cellulose (LC), unprotected cellulose (C), and extractives (E), with mass loss from each pool an exponential decay function affected by annual evapotranspiration (AET). The carbon loss is then partitioned into leached C or mineralized C depending upon the pool type and whether the litter is hardwood or coniferous (proportion leached: LC, 0.19 or 0.34; C, 0.14 or 0.21; E, 0.05 or 0.07). Thus, it appears that DOCMOD would not be able to distinguish leaching-related losses for Canadian sites with similar AET but different winter precipitation.

#### Fit of separate exponential-decay models to time-series data

Decomposition rate constants were calculated for the entire 6-year period for each litter type at each site, using the annual mass remaining data. As a first approximation, decomposition was assumed to follow a simple single-exponential decay model (after Olson 1963):

**Fig. 3.** Relationship between percent mass remaining after 6 years and the acid-unhydrolyzable residue to N ratio (AUR/N) among the 11 litter types; type letter codes are as in Table 2. Although only mean values for each type are plotted, regression equations were developed using data for all types and sites (Table 3). Lines plotted for regressions excluding (solid lines) or including wood (broken lines) illustrates the strong influence of wood.



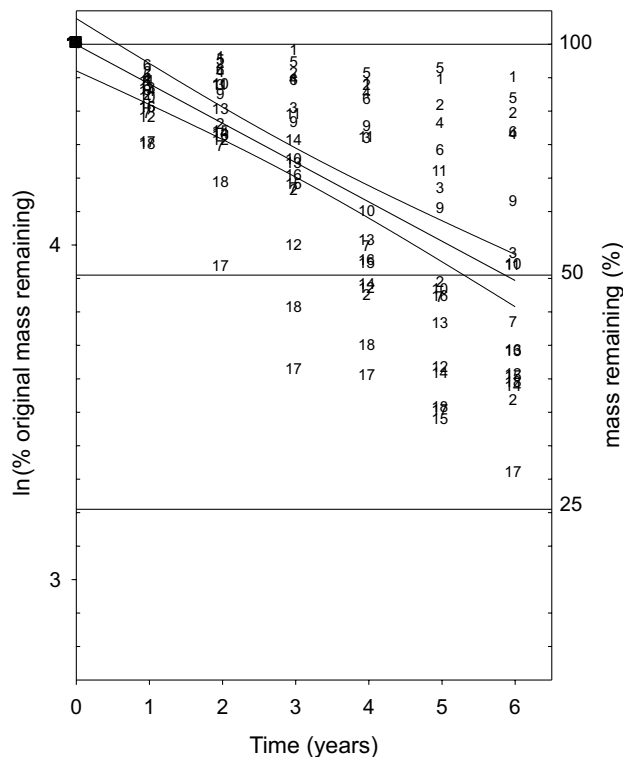
$$[1] \quad \text{Mass remaining (\%)} = 100 e^{-kt}$$

Decay constants were estimated by fitting a regression line through the natural logarithm ( $\ln$ ) of the percent mass remaining data over time with the intercept of the regression line assumed to go through  $\ln(100\%) (= 4.605)$  at time 0:

$$[2] \quad \ln(\% \text{ mass remaining}) = a - kt$$

Examination of scatterplots for each litter type revealed that some litter types deviated significantly from this simple model. For example, while western redcedar appeared to fit the single-exponential decay model (Fig. 4); fescue did not (Fig. 5). For western redcedar the intercept for the overall regression across all sites (4.598) did not differ from 4.605, while the intercept for fescue (4.325) did at  $p < 0.05$ . Thus, for all subsequent analyses a modified single-exponential decay model was fit for each litter type at each site (198 equations); this allowed the intercept to float and to be estimated

**Fig. 4.** Plot of the western redcedar  $\ln(\%$  mass remaining) over the 6-year period for all 18 sites; site numbers are as in Table 1. An overall regression line (and lines of 95% confidence limits) fitted through the data passes through the origin, 4.605, (i.e., 100%) at year 0, illustrating that for western redcedar only the decay constant ( $K_f$ ) (Table 5) varies with site.

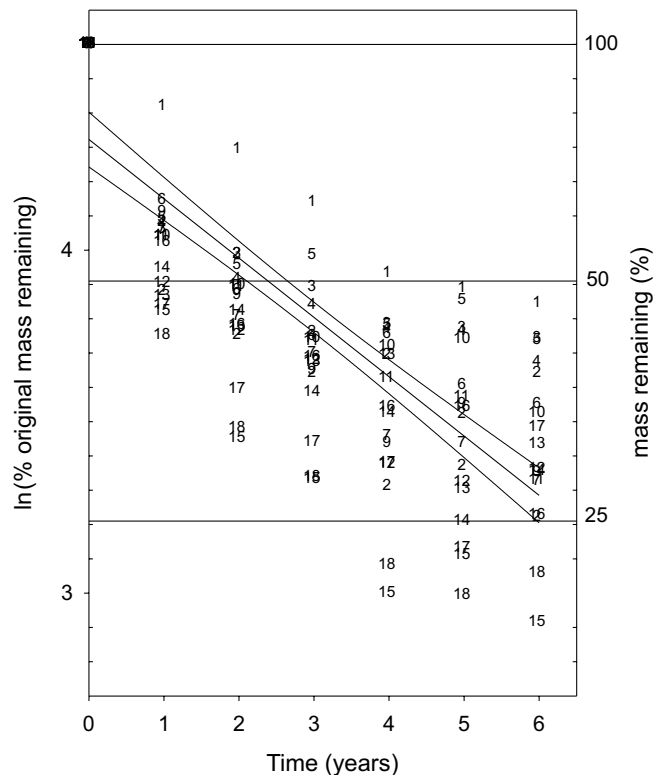


by regression. This effectively gives a two-phase model with decay rates in the first year higher than in subsequent years.

The decay constants,  $K_f$ , of the exponential decay equations covered a wide range of values from less than  $-0.005$  (wood blocks at Gillam and Inuvik) to  $0.30$  (white birch and black spruce at Morgan Arboretum) (Table 5) with differences due to both site and litter type. Intercepts,  $A$ , covered a narrower range of values and were more similar within a litter type than within a site. For example,  $A$  values for western redcedar ranged from  $4.46$  to  $4.67$  across all sites, while  $A$  values for Rocky Harbour ranged from  $4.21$  to  $4.61$  across all litter types (Table 5). This confirms the finding observed for mass remaining at year 1, 3, and 6 (Table 4) that litter quality is a relatively more important factor than climate in controlling initial mass loss and that its importance declines in the following phase, at least within the range of climates examined. Litter-quality factors were especially important when wood was included in the analysis.

The fit of the single-exponential decay model with intercept was good for most foliar types ( $r^2 = 0.70$ – $0.98$  for 184 of the 198 equations) although poorest for low-quality litter materials especially on cold sites (e.g., western redcedar at Inuvik,  $r^2 = 0.35$ ; Whitehorse,  $r^2 = 0.57$ ; wood at Inuvik,  $r^2 = 0.14$ ; Whitehorse,  $r^2 = 0.46$ ) (Table 5). Inspection of the mass data for these sites and types revealed variation in mass remaining with time, with some years showing apparent increases from previous years. However, the generally good fit

**Fig. 5.** Plot of the fescue  $\ln(\%$  mass remaining) over the 6-year period for all 18 sites; site numbers are as in Table 1. An overall regression line (with lines of 95% confidence limits) fitted through the data does not pass through the origin, 4.605, (i.e., 100%) at year 0, illustrating that for fescue both the intercept (A) and decay constant ( $K_f$ ) (Table 5) varies with site.



for the majority of the litter types and sites suggests that for at least the first 6 years of litter decomposition at these sites the single-exponential decay model with intercept was a suitable functional form for describing the time-series data. This does not mean this functional form may be suitable at later years. Several authors (e.g., Weider and Lang 1982; Bunnell and Tait 1974) have suggested that multi-compartment models are more appropriate forms to describe long-term decomposition. Minderman (1968) and Melillo et al. (1989) have suggested that decomposition is related to the decay of individual chemical fractions in the litter, and this assumption forms the theoretical basis for many of the generalized models of litter decay currently in use (e.g., CENTURY, DOCMOD, MBL-GEN, GENDEC; Moorhead et al. 1999). Titus and Malcolm (1999) suggest from a chronosequence study of Sitka spruce (*Picea sitchensis* (Bong.) Carrière) litter decay over 7 years in Scottish clearcuts, that a four-phase model was the most appropriate form for describing their results. In their model the first phase was completed in less than 1 year (105 days); the second phase lasted through year 2; the third phase, in years 3–5; and the final phase, in years 6 and 7.

#### Overall exponential decay models of litter decomposition

To develop a more general overall model of litter decomposition across all sites and types, stepwise multiple regres-



**Table 5.** Results of fitting a single-exponential decay model with intercept for each litter type at each site (198 equations) using the  $\ln(\% \text{ mass remaining})$  data over the entire 6-year period.

Site, A, $K_f$ , and $r^2$ *	Aspen	Beech	Bracken fern	Black spruce	Douglas- fir	Fescue	Jack pine	Tamarack	White birch	Wood	Western redcedar
Rocky Harbour											
A	4.294	4.494	4.439	4.402	4.446	4.285	4.431	4.430	4.219	4.618	4.586
$K_f$	-0.156	-0.167	-0.163	-0.231	-0.178	-0.188	-0.182	-0.143	-0.178	-0.050	-0.175
$r^2$	0.755	0.924	0.884	0.905	0.805	0.815	0.927	0.870	0.753	0.821	0.974
Chapleau											
A	4.422	4.626	4.504	4.501	4.618	4.287	4.456	4.607	4.435	4.681	4.641
$K_f$	-0.183	-0.189	-0.212	-0.250	-0.199	-0.200	-0.191	-0.205	-0.267	-0.144	-0.173
$r^2$	0.839	0.977	0.897	0.948	0.970	0.838	0.922	0.980	0.852	0.784	0.960
Gander											
A	4.518	4.574	4.530	4.497	4.590	4.272	4.460	4.551	4.346	4.674	4.659
$K_f$	-0.180	-0.136	-0.161	-0.228	-0.202	-0.168	-0.158	-0.188	-0.175	-0.063	-0.163
$r^2$	0.977	0.974	0.932	0.943	0.972	0.758	0.904	0.936	0.811	0.806	0.973
Gillam 1											
A	4.514	4.546	4.573	4.585	4.606	4.362	4.579	4.546	4.521	4.603	4.591
$K_f$	-0.079	-0.048	-0.082	-0.089	-0.059	-0.153	-0.077	-0.049	-0.100	-0.002	-0.032
$r^2$	0.896	0.891	0.950	0.970	0.884	0.818	0.927	0.909	0.927	0.049	0.903
Hidden Lake											
A	4.390	4.601	4.522	4.557	4.574	4.347	4.516	4.580	4.437	4.663	4.605
$K_f$	-0.139	-0.145	-0.177	-0.264	-0.188	-0.190	-0.212	-0.167	-0.250	-0.070	-0.152
$r^2$	0.804	0.940	0.932	0.941	0.971	0.873	0.980	0.958	0.946	0.898	0.988
Inuvik											
A	4.542	4.549	4.538	4.574	4.569	4.560	4.567	4.556	4.529	4.586	4.573
$K_f$	-0.047	-0.021	-0.029	-0.044	-0.022	-0.132	-0.037	-0.028	-0.048	0.004	-0.014
$r^2$	0.831	0.594	0.603	0.935	0.656	0.965	0.875	0.743	0.760	0.141	0.351
Kananaskis											
A	4.516	4.589	4.564	4.575	4.645	4.370	4.526	4.601	4.564	4.647	4.638
$K_f$	-0.125	-0.085	-0.102	-0.168	-0.142	-0.179	-0.130	-0.119	-0.180	-0.055	-0.096
$r^2$	0.917	0.967	0.893	0.956	0.959	0.890	0.967	0.942	0.868	0.827	0.895
Morgan Arboretum											
A	4.431	4.532	4.569	4.542	4.606	4.208	4.568	4.539	4.356	4.734	4.644
$K_f$	-0.267	-0.211	-0.269	-0.301	-0.290	-0.248	-0.239	-0.196	-0.299	-0.163	-0.187
$r^2$	0.896	0.969	0.991	0.954	0.937	0.825	0.986	0.961	0.898	0.898	0.925
Montmorency											
A	4.389	4.544	4.509	4.451	4.536	4.355	4.489	4.516	4.290	4.666	4.572
$K_f$	-0.187	-0.144	-0.146	-0.196	-0.159	-0.194	-0.174	-0.138	-0.156	-0.064	-0.139
$r^2$	0.886	0.920	0.957	0.941	0.977	0.885	0.963	0.964	0.769	0.787	0.990
Nelson House 1											
A	4.512	4.561	4.605	4.571	4.611	4.335	4.560	4.571	4.540	4.658	4.589
$K_f$	-0.095	-0.058	-0.115	-0.095	-0.078	-0.127	-0.099	-0.069	-0.118	-0.023	-0.041
$r^2$	0.838	0.854	0.848	0.957	0.896	0.757	0.951	0.933	0.863	0.333	0.901
Prince Albert											
A	4.518	4.579	4.606	4.594	4.592	4.370	4.571	4.582	4.541	4.617	4.609
$K_f$	-0.097	-0.062	-0.117	-0.129	-0.063	-0.156	-0.095	-0.066	-0.110	-0.009	-0.050
$r^2$	0.907	0.971	0.985	0.984	0.966	0.844	0.976	0.946	0.939	0.324	0.885
Petawawa											
A	4.503	4.607	4.611	4.586	4.633	4.315	4.584	4.634	4.537	4.576	4.672
$K_f$	-0.221	-0.181	-0.274	-0.261	-0.217	-0.197	-0.230	-0.190	-0.284	-0.159	-0.186
$r^2$	0.946	0.971	0.924	0.985	0.938	0.842	0.961	0.974	0.913	0.806	0.938
Port McNeill											
A	4.317	4.453	4.442	4.297	4.421	4.177	4.322	4.343	4.275	4.623	4.464
$K_f$	-0.132	-0.148	-0.111	-0.221	-0.163	-0.178	-0.199	-0.168	-0.233	-0.061	-0.207
$r^2$	0.748	0.920	0.792	0.822	0.873	0.655	0.787	0.760	0.852	0.987	0.925

**Table 5** (concluded).

Site, A, $K_f$ , and $r^2$ *	Aspen	Beech	Bracken fern	Black spruce	Douglas- fir	Fescue	Jack pine	Tamarack	White birch	Wood	Western redcedar
Schefferville											
A	4.473	4.612	4.585	4.520	4.583	4.341	4.502	4.512	4.487	4.622	4.632
$K_f$	-0.105	-0.121	-0.136	-0.149	-0.110	-0.120	-0.089	-0.065	-0.189	-0.011	-0.095
$r^2$	0.886	0.934	0.953	0.962	0.923	0.748	0.847	0.875	0.937	0.623	0.921
Shawnigan Lake											
A	4.313	4.418	4.474	4.339	4.453	4.177	4.395	4.473	4.214	4.671	4.507
$K_f$	-0.177	-0.155	-0.201	-0.257	-0.210	-0.234	-0.235	-0.194	-0.261	-0.138	-0.182
$r^2$	0.845	0.870	0.955	0.912	0.887	0.795	0.936	0.937	0.859	0.923	0.924
Termundee											
A	4.489	4.649	4.551	4.545	4.591	4.367	4.538	4.572	4.545	4.656	4.593
$K_f$	-0.148	-0.123	-0.121	-0.143	-0.119	-0.189	-0.075	-0.099	-0.174	-0.047	-0.079
$r^2$	0.955	0.940	0.773	0.974	0.910	0.864	0.893	0.852	0.910	0.798	0.911
Topley											
A	4.461	4.563	4.626	4.589	4.624	4.329	4.617	4.586	4.511	4.621	4.619
$K_f$	-0.118	-0.089	-0.147	-0.210	-0.158	-0.143	-0.193	-0.141	-0.236	-0.032	-0.126
$r^2$	0.877	0.932	0.916	0.965	0.952	0.781	0.948	0.929	0.943	0.710	0.923
Whitehorse											
A	4.488	4.547	4.511	4.546	4.565	4.353	4.522	4.535	4.491	4.613	4.581
$K_f$	-0.065	-0.025	-0.036	-0.062	-0.030	-0.116	-0.045	-0.031	-0.058	-0.012	-0.018
$r^2$	0.794	0.660	0.645	0.877	0.782	0.737	0.811	0.701	0.764	0.461	0.573

\*A, intercept;  $K_f$ , decay constant;  $r^2$ , correlation coefficient.

sion was used to determine which of the litter-quality and climate variables would be useful regressors for estimating either A or  $K_f$  in the exponential decay with intercept equation. As expected, the best predictors for A were similar to those for mass remaining at year 1. The best three-variable model for A included two litter-quality variables, which differed if wood was included (AUR, AUR/N) or excluded (CARB, AUR/N) from the data, and WP30 (Table 6). Both the four- and five-variable models included additional litter-quality variables, but these increased  $r^2$  by only 4–5% or 2–3%, respectively. Regressors for the best three-variable model for  $K_f$  were identical to those noted for 6-year mass remaining, including T30, SP30, and AUR/N (Table 6). Additional litter-quality variables were included for four-, five-, and six-variable models, but these increased  $r^2$ 's by only 3–4, 2–3, and 1–2%, respectively (Table 6).

To test the overall fit to the data, the variables and parameter values for the A and  $K_f$  terms, which had been estimated independently, were combined into single equations. Four equations were compared: a seven-variable model with wood (independent, W7), a seven-variable without wood (independent, N7), a nine-variable model with wood (independent, W9), and a nine-variable model without wood (independent, N9) (Table 7). These equations were then used to predict  $\ln(\% \text{ MR})$  annually over years 1–6 which was then compared with the observed  $\ln(\% \text{ MR})$  ( $n = 1188$  including wood,  $n = 1080$  excluding wood). The fit of the four models, determined by regressing predicted versus observed  $\ln(\% \text{ MR})$  data, was generally good ( $r^2 = 0.75$ – $0.76$  for seven-variable models;  $r^2 = 0.77$ – $0.78$  for nine-variable models), although slopes deviated significantly from 1.0 (Table 8).

#### Sources of bias in the overall models

Examination of a residuals plot for the seven-variable models (Fig. 6, independent, W7; Fig. 7, independent, N7)

showed significant bias, with the models overestimating decay (less MR) at early stages and underestimating decay (more MR) at later stages. Potential sources of such bias could be due to one or more causes including (i) inadequacies of the negative single-exponential functional form to represent the decay process; (ii) incorrect parameter estimates for the regressor variables in the A and  $K_f$  terms, as regressions for each were done independently; and (iii) non-linear relationships between the climatic or litter-quality variables used and  $K_f$  or A.

As noted earlier, the exponential decay model with intercept gave a good fit for the majority of sites and types. Only low-quality litters on cold sites had poor fits, but since little mass loss would have occurred in these cases, their influence in the overall model fit would be small. To test for effects of bias due to functional form, comparisons were made of the overall fit to the data. Predicted  $\ln(\% \text{ MR})$  for each site and type for years 1–6 was calculated using the  $K_f$  and A values for all 198 individual equations (Table 5), and compared with the observed  $\ln(\% \text{ MR})$  ( $n = 1188$  with wood,  $n = 1080$  without wood). The fits were very good ( $r^2 = 0.95$  with wood,  $0.94$  without wood) (Table 8) and residuals plots (Fig. 6, 198 equations; Fig. 7, 180 equations) demonstrated no bias; thus, it is unlikely that the functional form was a cause of the bias in the overall “independent” models.

To test whether the bias resulted from the independent estimate of regression parameter values for  $K_f$  and A, a series of cross-product variables were created through multiplication of years of exposure (Y) with the same litter-quality and climatic variables used in the independent seven- and nine-variable models. Regression variable parameter values for the A and  $K_f$  terms in the combined models (simultaneous, W7; simultaneous, W7; simultaneous, N7; simultaneous, N9) were then estimated simultaneously through regression with the  $\ln(\% \text{ MR})$  data (Table 7). Inspection of the match-

**Table 6.** Multiple regression results for predicting the intercept ( $A$ ) and decay constant ( $K_t$ ) for 2- to 12-variable decay models for the 6 years of data using all climate and litter-quality variables.

		Variables and parameter estimates													
Intercept															
Model	$r^2$	$\Delta r^2$	$B_0$	$B_1$	$X_1$	$B_2$	$X_2$	$B_3$	$X_3$	$B_4$	$X_4$	$B_5$	$X_5$	$B_6$	$X_6$
With wood															
A, W1	0.374		4.272	0.0009	AUR										
A, W2	0.594	0.22	4.338	0.0009	AUR	-0.0002	WP30								
A, W3	0.693	0.10	4.337	0.0008	AUR	0.0010	AUR/N	-0.0002	WP30						
A, W4	0.740	0.05	4.239	0.0051	CARB	0.0006	AUR	0.0018	AUR/N	-0.0002	WP30				
A, W5	0.771	0.03	4.209	0.0043	CARB	0.0021	PHEN	0.0005	AUR	0.0017	AUR/N	-0.0002	WP30		
$K_f$ , W1	0.439		-0.126	-0.0096	T30										
$K_f$ , W2	0.585	0.15	-0.160	0.0007	AUR/N	-0.0096	T30	-0.0003	SP30						
$K_f$ , W3	0.645	0.06	-0.121	0.0007	AUR/N	-0.0099	T30	-0.0099	T30	-0.0003	SP30				
$K_f$ , W4	0.672	0.03	-0.342	0.0034	PHEN	0.0003	AHF	-0.0099	T30	-0.0003	SP30				
$K_f$ , W5	0.664	0.02	-0.160	0.0005	ASH	0.0010	AUR/N	-0.0099	T30	-0.0003	SP30				
No wood															
A, N1	0.385		4.291	0.0061	AUR/N										
A, N2	0.674	0.29	4.364	0.0061	AUR/N	-0.0002	WP30								
A, N3	0.734	0.06	4.258	0.0053	CARB	0.0058	AUR/N	-0.0002	WP30						
A, N3a	0.771	0.04	4.173	0.0032	PHEN	0.0012	ASH	0.0009	AUR	-0.0002	WP30				
A, N4	0.763	0.03	4.242	0.0046	CARB	0.0004	AUR	0.0038	AUR/N	-0.0002	WP30				
A, N5	0.784	0.02	4.219	0.0043	CARB	0.0018	PHEN	0.0005	AUR	0.0025	AUR/N	-0.0002	WP30		
A, N6	0.791	0.01	4.103	0.0041	CARB	0.0032	PHEN	0.0002	AHF	0.0004	AUR	0.0025	AUR/N	-0.0002	WP30
$K_f$ , N1	0.507		-0.133	-0.0098	T30										
$K_f$ , N2	0.579	0.07	-0.092	-0.0101	T30	-0.0003	SP30								
$K_f$ , N3	0.607	0.03	-0.127	0.0011	PHEN	-0.0101	T30	-0.0003	SP30						
$K_f$ , N3a	0.607	0.03	-0.128	0.0010	AUR/N	-0.0101	T30	-0.0003	SP30						
$K_f$ , N4	0.643	0.04	-0.291	0.0029	PHEN	0.0003	AHF	-0.0101	T30	-0.0003	SP30				
$K_f$ , N5	0.664	0.02	-0.224	0.0012	PHEN	0.0008	ASH	0.0002	AUR	-0.0101	T30	-0.0003	SP30		
$K_f$ , N6	0.671	0.01	-0.247	0.0016	PHEN	0.0011	ASH	0.0003	AUR	-0.0011	AUR/N	-0.0101	T30	-0.0003	SP30

**Note:** Regressions for  $A$  and  $K_t$  were done independently including (W) wood ( $n = 198$ ) or excluding (N) wood ( $n = 180$ ). Within each group of models the  $\Delta r^2$  is the incremental change in  $r^2$  from a model with one less regression variable ( $X_i - 1$ ). Variables are as defined in Table 3. AHF, acid-hydrolyzable fraction.

**Table 7.** Final set of seven- or nine-variable overall decay models for predicting  $\ln(\%$  mass remaining) (LNMR) resulting from multiple regression analysis of data including (with, W) wood ( $n = 198$ ) or excluding (no, N) wood ( $n = 180$ ) and using all litter-quality and climate variables.

Model	Term	Equation
<b>With wood</b>		
Independent, W7	A	$\text{LNMR} = (4.336\ 70 + 0.000\ 75 \times \text{AUR}) + (0.001\ 03 \times \text{AUR/N}) + (-0.000\ 16 \times \text{WP30}) + (-0.120\ 90 + 0.000\ 75 \times \text{AUR/N}) + (-0.009\ 91 \times \text{T30}) + (-0.000\ 27 \times \text{SP30}) \times Y$
	$K_f$	
Independent, W9	A	$\text{LNMR} = (4.239\ 00 + 0.005\ 08 \times \text{CARB}) + (0.00060 \times \text{AUR}) + (0.001\ 78 \times \text{AUR/N}) + (-0.000\ 16 \times \text{WP30}) + (-0.159\ 50 + 0.000\ 50 \times \text{ASH}) + (0.000\ 98 \times \text{AUR/N}) + (-0.009\ 91 \times \text{T30}) + (-0.000\ 27 \times \text{SP30}) \times Y$
	$K_f$	
Simultaneous, W7	A	$\text{LNMR} = (4.149\ 74 + 0.000\ 97 \times \text{AUR}) + (0.002\ 23 \times \text{AUR/N}) + (-0.000\ 17 \times \text{WP30}) + (-0.092\ 36 \times Y) + (0.000\ 44 \times \text{YAUR/N}) + (-0.009\ 73 \times \text{YT30}) + (-0.000\ 25 \times \text{YSP30})$
	$K_f$	
Simultaneous, W9	A	$\text{LNMR} = (3.940\ 83 + 0.009\ 01 \times \text{CARB}) + (0.000\ 85 \times \text{AUR}) + (0.003\ 45 \times \text{AUR/N}) + (-0.000\ 17 \times \text{WP30}) + (-0.133\ 16 \times Y) + (0.000\ 52 \times \text{YASH}) + (0.000\ 68 \times \text{YAUR/N}) + (-0.009\ 73 \times \text{YT30}) + (-0.000\ 25 \times \text{YSP30})$
	$K_f$	
Best simultaneous, W7	A	$\text{LNMR} = (3.955\ 80 + 0.013\ 60 \times \text{CARB}) + (0.004\ 49 \times \text{AUR/N}) + (-0.263\ 60 \times Y) + (0.003\ 03 \times \text{YPHEN}) + (0.000\ 25 \times \text{YACID}) + (-0.011\ 40 \times \text{YT30}) + (-0.000\ 29 \times \text{YSP30})$
	$K_f$	
Best simultaneous, W9	A	$\text{LNMR} = (3.968\ 80 + 0.010\ 80 \times \text{CARB}) + (0.000\ 57 \times \text{AUR}) + (0.003\ 65 \times \text{AUR/N}) + (-0.000\ 17 \times \text{WP30}) + (-0.277\ 90 \times Y) + (0.002\ 99 \times \text{YPHEN}) + (0.000\ 26 \times \text{YACID}) + (-0.009\ 72 \times \text{YT30}) + (-0.000\ 25 \times \text{YSP30})$
	$K_f$	
<b>No wood</b>		
Independent, N7	A	$\text{LNMR} = (4.257\ 50 + 0.005\ 34 \times \text{CARB}) + (0.005\ 79 \times \text{AUR/N}) + (-0.000\ 18 \times \text{WP30}) + (-0.128\ 20 + 0.001\ 03 \times \text{AUR/N}) + (-0.010\ 10 \times \text{T30}) + (-0.000\ 28 \times \text{SP30}) \times Y$
	$K_f$	
Independent, N9	A	$\text{LNMR} = (4.242\ 40 + 0.004\ 62 \times \text{CARB}) + (0.000\ 39 \times \text{AUR}) + (0.003\ 78 \times \text{AUR/N}) + (-0.000\ 18 \times \text{WP30}) + (-0.290\ 50 + 0.002\ 89 \times \text{PHEN}) + (0.000\ 27 \times \text{ACID}) + (-0.010\ 10 \times \text{T30}) + (-0.000\ 28 \times \text{SP30}) \times Y$
	$K_f$	
Simultaneous, N7	A	$\text{LNMR} = (3.847\ 43 + 0.012\ 44 \times \text{CARB}) + (0.010\ 66 \times \text{AUR/N}) + (-0.000\ 19 \times \text{WP30}) + (-0.068\ 88 \times Y) + (-0.000\ 19 \times \text{YAUR/N}) + (-0.009\ 94 \times \text{YT30}) + (-0.000\ 26 \times \text{YSP30})$
	$K_f$	
Simultaneous, N9	A	$\text{LNMR} = (3.964\ 28 + 0.010\ 42 \times \text{CARB}) + (0.000\ 34 \times \text{AUR}) + (0.006\ 09 \times \text{AUR/N}) + (-0.000\ 19 \times \text{WP30}) + (-0.280\ 40 \times Y) + (0.002\ 91 \times \text{YPHEN}) + (0.000\ 28 \times \text{YACID}) + (-0.009\ 95 \times \text{YT30}) + (-0.000\ 26 \times \text{YSP30})$
	$K_f$	
Best simultaneous, N7	A	$\text{LNMR} = (3.560\ 80 + 0.007\ 71 \times \text{PHEN}) + (0.004\ 33 \times \text{ASH}) + (0.001\ 62 \times \text{AUR}) + (-0.000\ 19 \times \text{WP30}) + (-0.075\ 60 \times Y) + (-0.009\ 95 \times \text{YT30}) + (-0.000\ 26 \times \text{YSP30})$
	$K_f$	
Best simultaneous, N9	A	$\text{LNMR} = (3.839\ 10 + 0.004\ 94 \times \text{CARB}) + (0.007\ 30 \times \text{PHEN}) + (0.001\ 44 \times \text{AUR}) + (-0.000\ 34 \times \text{WP30}) + (-0.150\ 80 \times Y) + (0.000\ 95 \times \text{YASH}) + (-0.010\ 60 \times \text{YT30}) + (-0.000\ 28 \times \text{YSP30}) + (0.000\ 05 \times \text{YWP30})$
	$K_f$	

**Note:** For independent models, regressions for the A and  $K_f$  terms were done separately; hence, parameter values were estimated independently. For the simultaneous models cross-product variables were created (years  $\times$  climate or litter quality variable, e.g., YAUR/N, years  $\times$  AUR/N ratio) using the same variables as for the independent models; hence, regression estimates for parameter values were simultaneous. For the best simultaneous models all cross-product, climate, and litter-quality variables were included and variables and parameter values selected that gave the best fit. Variables are as defined in Table 3. Y, years.

**Table 8.** Comparison of decay models (independent, simultaneous, and best simultaneous models from Table 7; or all 198 or 180 equations from Table 5) fit by regression of predicted versus observed  $\ln(\%$  mass remaining) including (with, W) wood or excluding (no, N) wood.

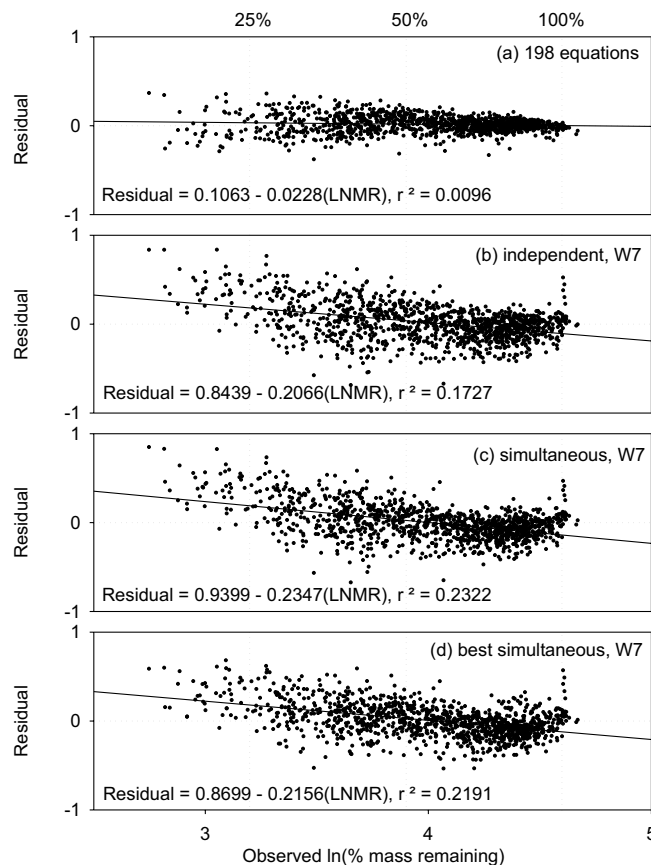
Model	<i>n</i>	$r^2$	$B_0$	$B_1$
<b>With wood</b>				
Independent, W7	1188	0.75	0.84	0.79
Independent, W9	1188	0.78	0.78	0.81
Simultaneous, W7	1188	0.76	0.94	0.76
Simultaneous, W9	1188	0.79	0.82	0.79
Best simultaneous, W7	1188	0.79	0.87	0.78
Best simultaneous, W9	1188	0.81	0.75	0.81
198 equations	1188	0.95	0.11	0.98
198 equations	4723	0.83	0.70	0.83
Best simultaneous, W7	4723	0.68	1.29	0.68
<b>No wood</b>				
Independent, N7	1080	0.76	0.80	0.80
Independent, N9	1080	0.79	0.75	0.82
Simultaneous, N7	1080	0.78	0.88	0.78
Simultaneous, N9	1080	0.80	0.78	0.80
Best simultaneous, N7	1080	0.80	0.78	0.80
Best simultaneous, N9	1080	0.81	0.76	0.81
180 equations	1080	0.94	0.08	0.98
180 equations	4297	0.83	0.65	0.84
Best simultaneous, N7	4297	0.71	1.16	0.70

**Note:** Regressions were of the following form: predicted =  $B_0 + B_1(\text{observed})$ . Most comparisons were made using the mean (10 or 11 types  $\times$  18 sites  $\times$  6 years) data ( $n = 1188$  or 1080). Comparisons with the entire data set (including the four within-site replicates, except for missing bags) were done for the 198 or 180 equations for each type and site and for the best fit seven-variable decay model (best simultaneous).

ing simultaneous and independent equations demonstrated that parameter values did change if parameter estimates were made simultaneously. For example, in the independent, W7 equation the parameter value for AUR in the A term (0.00075) was smaller than the same parameter in the simultaneous, W7 equation (AUR = 0.00097). Simultaneous estimates of parameter values for the  $K_f$  and A terms (simultaneous models) resulted in slight improvements in overall fit, with the  $r^2$ 's 1–2% higher than the independent parameter estimate models (Table 8, independent models). However, the residuals plots demonstrated that the “simultaneous” models were still biased (Fig. 6, simultaneous, W7; Fig. 7, simultaneous, N7), indicating that while simultaneous estimate of parameters slightly improved fit it could not account for model bias in the independent models.

Since there were such changes in parameter values with the simultaneous versus independent parameter estimates, the independent regression for the  $K_f$  and A terms could also have resulted in inappropriate selection of variables and, thus, serve as another source of bias. To test for this, a complete set of cross-product variables was created using all the litter-quality and climate variables used in the initial stepwise multiple regression for A and  $K_f$ , and the best seven- and nine-variable models (best simultaneous) were derived by stepwise multiple regression on the  $\ln(\%$  MR) data (Table 7). The variables selected differed from those selected in the initial stepwise regression (independent models). For ex-

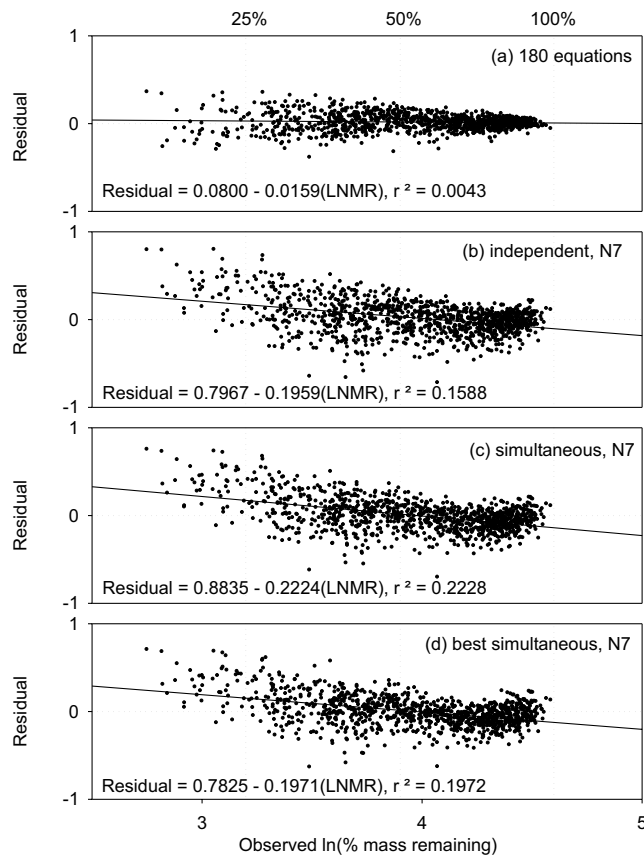
**Fig. 6.** Residuals plots (predicted vs. observed  $\ln(\%$  mass remaining)) for four decay models using data for years 1–6, 18 sites, and 11 types, including wood (W): (a) 198 equations (Table 5); (b) independent, W7; (c) simultaneous, W7; (d) best simultaneous, W7. See Table 7 for details on latter three models. Regressions through residuals with intercepts or slopes different from 0 indicate degree of constant or variable bias, respectively.



ample, for models with wood the best seven-variable model (best simultaneous, W7) only included two litter-quality variables and no climate variables in the A term, while the  $K_f$  term included two different litter-quality variables (Table 7). The best nine-variable model with wood (best simultaneous, W9) included the same set of variables (CARB, AUR, AUR/N, WP30) in the A term as the nine-variable independent model, and the same two climate variables (T30, SP30) in the  $K_f$  term, but two different litter-quality variables (PHEN, ACID). The best simultaneous models resulted only in slight improvements of fit with  $r^2$ 's 1–2% higher than the comparable simultaneous models (Table 8). However, the residuals plots (Fig. 6, best simultaneous, W7; Fig. 7, best simultaneous, N7) indicate that the models were still biased.

Sources of bias in the overall model are still unexplained. Nonlinearities between litter-quality or climatic variables and  $K_f$  or A, might still be present and not detected in this analysis. One obvious nonlinear relationship was with AUR/N when wood was included (e.g., Fig. 3). Although wood acts as an outlier, it does not account for the bias, which still persists even when wood was excluded during model parameter estimation and from comparisons of pre-

**Fig. 7.** Residuals plots (predicted vs. observed  $\ln(\%$  mass remaining mass)) for four decay models with data for years 1–6, 18 sites, and 10 types, excluding wood (N): (a) 180 equations (Table 5); (b) independent, N7; (c) simultaneous, N7; (d) best simultaneous, N7. See Table 7 for details on latter three models. Regressions through residuals with intercepts or slopes different from 0 indicate degree of constant or variable bias, respectively.



dicted versus observed LNMR (e.g., Fig. 6, best simultaneous, W7 and Fig. 7, best simultaneous, N7 both show bias). Earlier examination of scatterplots of the litter-quality or climatic variables and  $K_f$  or  $A$  had revealed a nonlinearity between  $A$  and P30 which was eliminated when WP30 was used. Examination of other scatterplots did not reveal any other obvious nonlinearities; thus, the bias in the overall models was likely related to their inability to capture effects resulting from specific sites or litter types.

#### Best overall empirical model

At present the best overall empirical model for describing the percent mass remaining over 6 years for all sites and types is best simultaneous, W9 or best simultaneous, N9 (Table 7) using the correction for bias (Table 8). The best simultaneous seven- or nine-variable models give good fits to the data ( $r^2 = 0.78\text{--}0.80$ ) but still explained 14% less variance than that obtained using the 198 individual equations ( $r^2 = 0.94$ ). Regressions of predicted and observed  $\ln(\%$  MR) for the entire data set ( $n = 4723$  with wood,  $n = 4297$  no wood) using both best simultaneous seven-variable ( $r^2 = 0.68$  including wood,  $r^2 = 0.70$  excluding wood) and all 198 or 180 equations ( $r^2 = 0.82$  including wood,  $r^2 = 0.83$  excluding wood) demonstrates that about 10–12% of the entire

variance is due to within-site variation (Table 8). To find an unbiased model that better fits the observed data will likely require the use of other factors and variables to account for differences among the sites and litter types. For example, wood was noted as an outlier when compared with the foliar litters, and its exclusion changed variables used in the overall decay model and improved the models' fit ( $r^2$  increased by 1%, Table 8).

#### Possible reasons for the influence of winter precipitation

As noted earlier for year-1 mass loss, the effect of winter precipitation might be related to its role in leaching. Although many simulation models that use daily or monthly weather data would have the capability of including the effects of winter precipitation on leaching losses, few if any do so. None of the empirical models from other studies examined for this paper appear to have considered WP as a climatic variable. In analyses of pine or spruce litter decomposition across a climatic transect extending from Denmark to northern Sweden, Berg et al. (1993, 2000) found that although first-year mass loss in pine stands was strongly related to AET, first-year mass loss in spruce stands along the same transect was only weakly related to AET. Berg et al. (2000) speculates that the differences in the climatic effects on mass loss between the pine and spruce stands might be related to differences in canopy cover. Spruce, which have much denser canopies, might have similar ground microclimates along the transect, and thus, mass loss would be only weakly related to the climatic variables. Furthermore, Berg et al. (2000) suggest that the microclimate effect might be due to water limitations arising from interception by the dense spruce canopies. If winter precipitation is important, and snow interception is greater and less variable in the dense spruce stands than in the sparser pine stands, then mass loss in spruce stands would be lower and less variable across the climatic gradient.

In CIDET, first-year mass remaining or  $A$  values were lower for sites with higher winter precipitation. The two Newfoundland sites (Gander, Rocky Harbour) followed this overall trend but contrasted sharply with each other. While both sites received similar amounts of precipitation (WP30, SP30, or P30) and had similar temperatures, first-year mass remaining and  $A$  values were much lower in Rocky Harbour and well below the overall trends. These site differences might be related to degree of WP intercepted by the trees and canopy cover. The Gander site has a dense black spruce (*Picea mariana*) stand (basal area (BA) 61.7 m<sup>2</sup>) while Rocky Harbour has a sparser stand of balsam fir (*Abies balsamea* (L.) Mill.) (BA 15.4 m<sup>2</sup>) and white birch (*Betula papyrifera*) (BA 2.8 m<sup>2</sup>).

#### Conclusions

Litter and wood mass has continued to decline over the entire 6-year period for all plant tissue types at all sites. The amount of mass remaining at 6 years could be effectively predicted with a relatively limited range of climate (temperature and summer precipitation) and litter-quality (AUR and AUR/N) variables. Wood, however, was an outlier compared with the foliar litters; it had an initial AUR/N nearly three times higher and a percent mass remaining 20% greater than

the next closest litter type, and thus, data analyses and model development should be done with values for wood excluded from the data.

A single-exponential decay equation with intercept worked surprisingly well for predicting MR over 6 years for each site and litter type. This was reflected in the comparisons of predicted vs. observed  $\ln(\% \text{ MR})$  using all 198 equations, which explained over 90% of the variance in the site by type mean data ( $n = 198$ ) and over 80% of the variance in the entire data ( $n = 4723$ ). The use of a floating intercept was able to account for the more rapid initial phase of decomposition occurring in the first year for some litter types. The equations should not, however, be used for predicting MR at less than 1 year, as for some litter types predicted mass remaining at year 0 was greater than 100%. The usefulness of this equation's functional form will likely decrease in future years, since the final phase of litter decomposition usually has much reduced rates of decay (e.g., Weider and Lang 1982; Bunnell and Tait 1974).

The best set of variables for predicting decomposition changed over the 6-year period. This was reflected in both the analysis of the mass remaining data at 1, 3, and 6 years and in the analysis of variables for  $A$  and  $K_f$  of the overall single-exponential decay model with intercept. Litter-quality factors and winter precipitation were important in predicting decomposition within the first year, while temperature, summer precipitation, and a variety of litter-quality factors including AUR/N were useful in subsequent years.

The finding that winter precipitation was an important factor affecting decomposition within the first year needs further study. We suggest that this effect may be due to mass loss from leaching of soluble compounds or due to leaching of soluble phenolics that might be inhibiting litter decay. Leaching would be higher in areas with greater winter precipitation, occurring either as rain (western coastal temperate sites) or as large snowfall accumulations, which would give rise to greater spring snowmelt (eastern wet boreal sites).

Although the overall decay models were effective at explaining mass remaining over the entire 6-year period ( $r^2 = 0.79\text{--}0.81$ ) the models required corrections for bias, as they overestimated initial mass loss and underestimated later mass loss. The bias was unrelated to the way the models were developed, although simultaneous selection and parameter estimation of model variables does improve model fit and should be the method used for future model development. It appears that site- and type-specific factors unaccounted for in the climate and litter-quality variables used were the likely causes of model bias and limitations in model fit. Such factors include in situ temperatures and possibly other measures of litter quality. Certainly temperatures at the soil surface within a site or under snow cover will be higher than air temperatures in the open field of a nearby weather station. Additional research is required to identify these factors and further the development of more generalized models of litter decomposition.

## Acknowledgments

Funding from the Climate Change and Ecosystem Processes Networks of the Canadian Forest Service supported this experiment. B. Ferris, R. Leach, and A. Harris provided

technical support. Ongoing field assistance was also provided by L. Kutny and D. White. The CIDET Working Group gratefully acknowledges past participants in this experiment, M. Weber, C. Monreal, D. Anderson, R. Trowbridge, and the late Steve Zoltai, for their encouragement and assistance including help in establishing sites or initial litter collection. Further information on CIDET is available on the Web at <http://www.pfc.cfs.nrcan.gc.ca/climate/cidet>.

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