

Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems

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Received October 21, 1989

ABER, J. D., MELILLO, J. M., and MCCLAUGHERTY, C. A. 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Can. J. Bot.* **68**: 2201–2208.

Long-term decomposition data are presented for several types of foliar and fine root litter in different stands in Wisconsin and Massachusetts, U.S.A. Changes in mass remaining as well as nitrogen and carbon fraction (extractives, cellulose, lignin) concentration are reported. Three models were developed for describing change in mass remaining with time: a litter-specific exponential decay function (statistical fit of data for each litter type), a generalized exponential decay function (k predicted from initial litter chemistry), and a carbon fraction model that calculates the weight loss of each carbon fraction individually as a function of current carbon chemistry regardless of litter type. The exponential decay function fits all litter data well for the portion of decomposition described here, but would not be appropriate for modeling longer term decomposition. Both the generalized and carbon fraction models predicted weight loss accurately. All litter types had similar carbon fraction chemistries at the end of the first phase of decomposition described here and also exhibited a narrow range of changes in nitrogen concentration per unit weight loss. It is concluded that the length of time required to convert litter into soil organic matter and the chemistry of the material produced by this process can be predicted from initial litter chemistry and (or) relatively short-term litter decay data.

Key words: immobilization, mineralization, humus, lignin, cellulose, extractives.

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Les auteurs présentent des données sur la décomposition à long terme pour plusieurs types de feuille et de racine dans différentes stations du Wisconsin et du Massachusetts, aux États-Unis. Les changements de la masse résiduelle ainsi que les concentrations des fractions azotées et carbonées (extractibles, cellulose, lignine) sont présentés. Pour décrire les changements temporels de la masse résiduelle, les auteurs présentent trois modèles : décomposition spécifique à la litière en fonction exponentielle (correspondance statistique des données pour chaque type de litière), décomposition générale en fonction exponentielle (k prédit à partir de la composition chimique initiale de la litière) et un modèle basé sur la fraction carbonée qui calcule la perte en poids de chaque fraction carbonée en fonction de la composition chimique carbonée courante, indépendamment du type de litière. La décomposition en fonction exponentielle rend compte de toutes les données sur les litières pour la partie de la décomposition décrite ici, mais ne serait pas utile comme modèle pour la décomposition à long terme. Le modèle généralisé aussi bien que le modèle basé sur la fraction carbonée permettent tous les deux de prédire avec précision la perte en poids. À la fin de la première étape de décomposition décrite ici, tous les types de litière montrent une composition chimique carbonée semblable et montrent de plus une étroite fourchette de variation dans la concentration azotée par unité de poids perdu. Les auteurs concluent que la durée requise pour convertir la litière en matière organique du sol et la composition chimique du matériel produit par ce processus peuvent être prédits à partir de la composition chimique initiale de la litière et (ou) à partir de données à court terme sur la décomposition.

Mots clés : immobilisation, minéralisation, humus, lignine, cellulose, extractibles.

[Traduit par la revue]

Introduction

Decomposition of litter is one of the most frequently studied processes in temperate forest ecosystems. However, the scope and duration of research performed to date is heavily skewed towards short-term studies of mass loss and, perhaps, dynamics of macronutrients. Relatively few studies have measured the long-term changes in either nutrients or the major carbon fractions (lignin, cellulose, extractives) in decaying litter. Those studies that have been done (e.g., Berg et al. 1982, 1984; Heal et al. 1981; Edmonds 1987; Melillo et al. 1989)

show that various combinations of litter quality as defined by carbon-fraction and nutrient-content data are good predictors of decay rate and nutrient dynamics.

Because most litter decay research is short-term, very few studies have dealt with the role of litter decay in the formation of stable forest soil organic matter or humus (e.g., Aber et al. 1982; McLaugherty and Berg 1987; cf. treatment of soil organic matter in CENTURY model of Parton et al. 1988). Rather, decomposition in litter and in soil organic matter have been studied as separate processes in forest ecosystems, using different techniques (e.g., on-site or laboratory incubations for

soil organic matter, litter bag studies for litter). Few attempts have been made to link these two processes. As a result, existing models of organic matter and nitrogen dynamics in forest ecosystems (e.g., Aber et al. 1982; Pastor and Post 1986; Kimmins and Scoullar 1979) use functions for transferring decayed litter into a humus compartment that are not strongly data based.

Organic matter decay is assuming increasing importance in the context of global change research or earth system science. Accurate predictions of alterations in carbon storage, nutrient dynamics, soil chemistry, and productivity of forest ecosystems as a result of climate change or atmospheric deposition will rely on a full, quantitative understanding of decomposition processes across the full continuum from fresh litter to soil organic matter and their relationship to controlling factors such as initial carbon fractions and nutrient content.

In previous papers we presented a framework for examining the interactions between mass loss and nitrogen dynamics in decaying litter and suggested a role for both carbon fractions and nitrogen content in determining these dynamics (Aber and Melillo 1980, 1982; Melillo et al. 1982; Melillo and Aber 1984). However, these papers relied on data from 1- or 2-year studies and did not cover the entire process to the formation of relatively stable soil organic matter. A recent paper (Melillo et al. 1989) discussed this full continuum based on 77-month decay data for red pine needles at the Harvard Forest in Petersham, MA, and discussed changes in carbon fraction chemistry and carbon isotope ratios over this sequence.

The purpose of this paper is to present additional long-term decay data from the Harvard Forest site and to combine these with data from a Wisconsin study (McClougherty et al. 1985) to develop a quantitative analysis of the litter to soil organic matter decay sequence. The express goal of this analysis is to develop equations for inclusion into ecosystem-level models of organic matter and nitrogen dynamics in forest ecosystems.

Weight loss data are analyzed (*i*) by using the standard exponential model for mass loss for each litter type (Olson 1963; Jenny et al. 1949), (*ii*) by predicting the decay constant (*k*) in the exponential decay equation from initial carbon fraction chemistry, and (*iii*) through a generalized model based on decay rates of different carbon fractions as a function of overall carbon quality within the different materials. The hypothesis implicit in the third approach is that carbon fractions determined by laboratory wet chemical analyses are good generalized predictors of decomposition that do not differ between litter types.

Nitrogen dynamics are analyzed within the framework of the inverse-linear relationship between mass loss and nitrogen concentration presented in earlier papers. We also attempt to predict the slope of this relationship, and therefore the pattern of nitrogen dynamics during decay, from initial carbon fraction and nitrogen content.

Methods

Field studies

Data used here are from two previously published studies, both using standard litter bag methods (Bocock et al. 1960; Gosz et al. 1973; Melillo et al. 1982). Additional unpublished data collected as part of these studies are presented here for the first time.

McClougherty et al. (1985) measured carbon chemistry and nitrogen content over a 5-year period for 12 different litter types, two litter bag mesh sizes, and two soil positions within five forests with contrasting nitrogen cycling rates on Blackhawk Island, Wisconsin

(Pastor et al. 1982, 1984). As results showed no significant differences by soil position or stand type over the first 2 years, we have used data from foliar and fine root litter types (total of eight) contained in fine (0.1 mm) mesh bags placed, with two exceptions, in the stand from which the litter types were collected (Table 1). The exceptions are red oak foliage and white pine fine roots, which were incubated in the sugar maple stand. For foliar litter, data from bags placed on the soil surface were used. Fine root data are from bags placed within the A horizon of the mineral soil. Fourteen collections were made over a 5-year period.

Melillo et al. (1989) presented data on the long-term decomposition of red pine needles in a red pine stand at the Harvard Forest, Petersham, MA (Aber et al. 1983). These data are part of a larger study involving four litter types and two stands (Table 1). All six of the available litter-stand combinations in Table 1 are included in this analysis. All litters were placed out in 2-mm mesh nylon bags. Fifteen collections covering 77 months were made.

Chemical analyses

Retrieved samples in both studies were dried (70°C), weighed, and subsampled for moisture content (105°C, 48 h) and ash content (500°C, 12 h) to determine percentage of original ash-free dry weight remaining. Total nitrogen content was determined by Kjeldahl digestion and analysis for ammonium content in digestate (Technicon Industrial Systems 1977).

Carbon fraction chemistry was measured differently in the two studies. McClougherty et al. (1985) used dichloromethane and hot water to remove nonpolar and polar extractives, respectively (Technical Association of the Pulp and Paper Industry 1975, 1976). The total of these two fractions will be called extractives in this paper. Residues were then subjected to a two-stage digestion in sulfuric acid (Effland 1977). Mass loss during digestion is termed the acid-soluble fraction and is roughly equivalent to holo-cellulose (cellulose plus hemicellulose) in initial material (this fraction will be called cellulose in this paper). Mass remaining is termed the acid-insoluble fraction and is functionally equivalent to lignin in initial material.

Melillo et al. (1989) used a modified Van Soest technique for all samples. All red pine samples were also analyzed using the same methods as the Wisconsin samples. In addition, an intercomparison of these two chemical methods determined that results from one can be used to predict results from the other, i.e., that the two are inter-comparable (Ryan et al. 1989). These results have been used to convert the Harvard Forest carbon chemistry data to their equivalent values by the McClougherty technique.

Statistical analyses

Mass loss and carbon fractions

Mass loss data were analyzed in three ways: (*i*) using the standard exponential equation, with *k* determined statistically for each litter type (litter-specific exponential model); (*ii*) using the *k* values determined in analysis *i* to develop regressions between *k* and initial carbon and nitrogen chemistry (generalized exponential decay model); and (*iii*) by developing an iterative model of mass loss and changes in carbon fraction chemistry using combined data from all litter types through time (carbon fraction model).

The exponential decay function

$$[1] \quad y = e^{-kt}$$

where *y* is the fraction of initial mass remaining, *t* is time, and *k* is the decay constant fit to each data set, has long been the most commonly used equation for describing litter decomposition. This assumes constant fractional mass loss with time. We fit the exponential equation separately to data for each litter type in Table 1 (litter-specific exponential model). We then regressed the derived *k* values against initial carbon fraction and nitrogen concentrations of all materials to develop a generalized exponential model that predicts mass loss directly from initial litter chemistry.

In addition, an iterative model was constructed based on the decay of specific carbon fractions within all materials as a function of litter

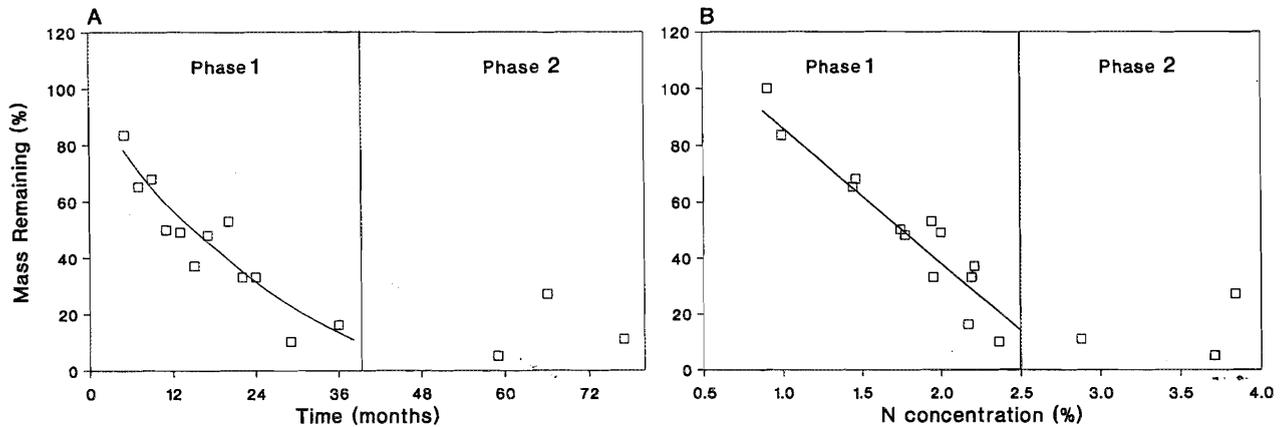


FIG. 1. Example of separation of decomposition data into phase 1 and phase 2 according to changes in decay rates and nitrogen dynamics. Decomposition data are for paper birch foliage litter in a mixed hardwood stand at the Harvard forest. (A) Mass remaining through time. (B) Mass remaining versus N concentration (the inverse-linear function). For both panels, phase 1 continues until mass remaining equals the mean mass remaining value for all points in phase 2.

TABLE 1. Characteristics of litter types used in this analysis

Location and litter type	Length of decay sequence (years)	No. of collections	Initial chemistry (%)			
			Lignin	Cellulose	Extractives	Nitrogen
Harvard Forest, hardwood stand						
Paper birch foliage	6.5	17	20.7	37.6	41.7	0.90
Red maple foliage	6.5	17	17.3	38.0	44.7	0.66
Red oak foliage	6.5	17	26.7	42.5	30.8	0.83
Harvard Forest, red pine stand						
Red maple foliage	6.5	17	17.2	38.9	43.9	0.68
Red oak foliage	6.5	17	28.2	43.4	28.4	0.84
Red pine foliage	6.5	17	27.7	46.5	25.8	0.43
Blackhawk Island, Wisconsin						
Sugar maple foliage	5.0	14	12.1	43.1	44.8	0.83
Aspen foliage	5.0	8	21.4	47.5	31.1	0.83
Red oak foliage	5.0	14	24.8	45.2	30.0	0.82
White oak foliage	5.0	8	20.2	47.4	32.4	0.84
Hemlock foliage	5.0	8	20.6	39.6	39.8	0.83
White pine foliage	5.0	8	22.5	44.7	32.8	0.44
White pine roots	5.0	8	25.3	49.5	25.2	0.93
Sugar maple roots	5.0	8	33.8	47.7	18.5	1.67

quality (carbon fraction model). For this analysis, data on annual changes in the mass of the three carbon fractions described above were pooled across litter types and regressed against indices of overall carbon quality of the material (e.g., lignin concentration, the ratio of lignin to lignin plus cellulose, i.e., the ligno-cellulose index or LCI of Melillo et al. 1989). Data for the 2nd and subsequent years of decay were compared with the carbon quality indices for the material at the beginning of that year, rather than with initial carbon quality data. The purpose of this approach was to produce a dynamic model of changes in carbon fractions through time that will depend only on current carbon quality parameters and can be iterated through time and lumped by litter type.

Nitrogen dynamics

In previous papers we described an inverse-linear relationship between the percentage of original mass remaining in decaying litter (y-axis) and its nitrogen concentration (x-axis) (Aber and Melillo 1980, 1982; see Fig. 1B below for an example). This relationship allows a direct calculation of the timing of the switch from immobilization to mineralization of nitrogen, the maximum nitrogen content of the material, and the amount of nitrogen immobilized per unit

mass loss (Aber and Melillo 1982). The inverse-linear relationship was shown to hold in most litter decay studies (Berg and McLaugherty 1987, 1989; Aber and Melillo 1980, 1982; Melillo et al. 1982, 1989) and also across climatic and pollution gradients, which alter rates of decay but not the slope of this relationship (Melillo and Aber 1984; Strojan 1978).

The strong linearity of this relationship allows prediction of the future course of carbon-nitrogen dynamics from relatively short-term decay data. However, it has not been known how far into the decay process (to what percentage of original mass remaining) this linear relationship holds.

Results

General patterns

Melillo et al. (1989) described a two-phase decay sequence for long-term red pine decay data. Similar results were obtained for all litter types in this study (e.g., Fig. 1). The first phase shows relatively constant fractional mass loss, whereas mass loss becomes imperceptible in the second phase (Fig. 1A). This switch in mass loss rate coincides with a deviation from the

TABLE 2. Calculated characteristics of decay rate, N dynamics, and phase 1 end point for all litter types

Location and litter type	<i>k</i>	Mass loss time in phase 1 (years)			Inverse-linear			At end of phase 1		
		<i>k</i>	GK	CF	Intercept	Slope	<i>R</i> ²	% mass remaining	LCI	%N
Harvard Forest, hardwood stand										
Paper birch foliage	0.628	3.2	3.0	3-4	142.1	-52.0	0.90	13.8	0.50	2.49
Red maple foliage	0.700	2.3	2.3	3-4	112.4	-43.0	0.83	19.5	0.48	2.25
Red oak foliage	0.395	4.3	4.0	4-5	142.1	-54.2	0.98	18.3	0.49	2.28
Harvard Forest, red pine stand										
Red maple foliage	0.714	2.6	2.6	3-4	106.9	-41.6	0.83	15.8	0.45	1.97
Red oak foliage	0.402	4.4	4.8	4-5	153.5	-63.0	0.99	16.9	0.48	2.17
Red pine foliage	0.329	5.4	5.6	4-5	120.5	-66.0	0.95	17.0	0.46	1.52
Blackhawk Island, Wisconsin										
Sugar maple foliage	0.828	2.1	2.4	2-3	130.1	-46.5	0.95	17.3	0.51	2.42
Aspen foliage	0.515	2.9	3.5	3-4	125.7	-35.4	0.94	22.3	0.54	2.77
Red oak foliage	0.338	4.4	3.7	3-4	137.1	-40.5	0.97	22.7	0.55	2.82
White oak foliage	0.424	3.7	3.5	3-4	127.1	-38.9	0.93	20.6	0.45	2.20
Hemlock foliage	0.358	4.5	2.6	3-4	165.1	-69.0	0.95	(20)	(0.48)	(1.79)
White pine foliage	0.360	3.7	2.9	3-4	123.1	-60.5	0.93	26.1	0.47	1.40
White pine roots	0.300	5.3	5.3	4-5	134.8	-42.3	0.77	(20)	(0.55)	(2.30)
Sugar maple roots	0.204	7.9	10.2	5-6	161.8	-44.1	0.85	(20)	(0.60)	(3.07)

NOTE: LCI at end of phase was calculated using the carbon fraction model. All other values are from field data. The first *k* value is exponential decay constant fit to time series data. The second *k* value, GK, and CF refer to estimates obtained from the litter-specific exponential, generalized exponential, and carbon fraction models, respectively. All regressions for the inverse-linear relationship are significant at the 0.05 level. Values in parentheses are estimates for litter types for which data do not reach the end of phase 1.

inverse-linear relationship between mass loss and nitrogen concentration that holds through the first phase (Fig. 1B; for purposes of defining the phases, all points for which the measured mass remaining is higher than predicted by the inverse-linear relationship by more than twice the standard error of that regression, or for which the predicted mass remaining would be negative, are included in phase 2).

Data from this study are not sufficient to describe changes in the second phase. Indeed, litter bag techniques may be inappropriate for characterizing the second phase, in which both our data and decomposition theory would suggest that mass loss is very slow. Because of this, the remainder of the analyses presented here will deal with the characteristics of the first phase, which generally includes about 80% of mass loss (see below). Statistical analyses discussed here involve only points from the first phase of decay unless specifically stated otherwise.

Rates of mass loss

The exponential decay function provided a good fit to mass loss for phase 1 data for all litter types (Table 2). Only the two red maple series from the Harvard Forest showed significantly nonlinear residuals with time for the exponential equation form. It should be emphasized here that an exponential decay curve, especially derived from short-term decay data, would greatly overestimate the rate of decay of the soil organic matter (phase 2 material) produced from each litter type.

The *k* parameter in the exponential decay equations for all litter types was strongly correlated with initial lignin concentration but more strongly with lignin plus cellulose concentration (equivalent to 1.0 minus the extractive concentration; Tables 1, 2; Fig. 2). The only outlier is hemlock needle litter, which decays more slowly than would be predicted by the regression.

The carbon fraction model is based on three equations predicting mass loss per fraction as a function of current LCI

(lignin/(lignin + cellulose)). This index of overall litter carbon quality was a better predictor of carbon fraction change than any single carbon fraction value or any other combination of carbon and nitrogen values.

Decomposition of the extractive fraction was very strongly and inversely related to current LCI (Fig. 3A). Lignin decay is somewhat less strongly related to current LCI, and the slope is positive, indicating increased lignin decomposition rate with increasing LCI (Fig. 3B). Potential reasons for this relationship are discussed below. Data from fine root litter contribute three of the apparent outliers in this relationship. The relationship between LCI and cellulose decay is the weakest of the three but still significant (Fig. 3C).

Because it is based on annual time-step data, the carbon fraction model could not be run on shorter time steps, as a bias would result from cumulative changes in litter quality with more frequent iterations. Therefore, we compared mass remaining at year 1 and 2, as calculated from the litter-specific exponential model, with values predicted by the carbon fraction model using only initial carbon fraction chemistry for all 16 litter types (Fig. 4A). The same comparison was made between the litter-specific and generalized exponential models (Fig. 4B). Results show that the generalized exponential model is slightly more accurate than the carbon fraction model (standard error of the estimate (SEE) = 0.062 vs. 0.088, respectively; hemlock data removed from generalized exponential model).

Nitrogen dynamics

All litter types showed highly significant ($p < 0.01$) fits for the inverse-linear relationship between percentage of original mass remaining and percent nitrogen (Table 2; see Fig. 1B for example). Slope was not significantly correlated ($p > 0.05$) with any single litter chemistry parameter nor with any linear combination or ratios of these variables. This lack of correlation is partially due to the low range of slope values calculated (SD = 10.99; Table 2).

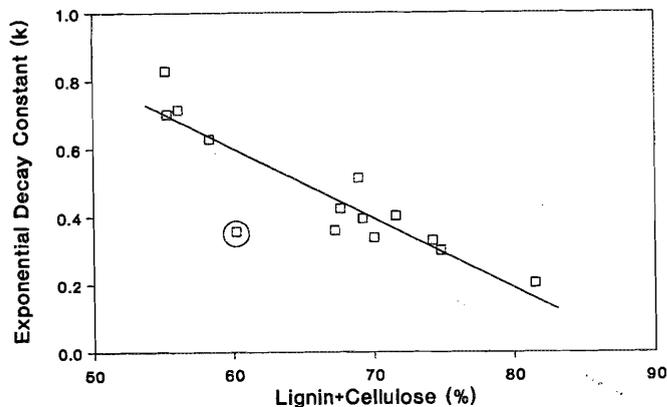


FIG. 2. Exponential decay constant (k) versus initial lignin plus cellulose fractions for the 14 litter types used in this study. Hemlock needle data are circled. The line is the regression equation with hemlock needle litter excluded ($k = 1.92 - 0.0216$ (lignin plus cellulose), $R^2 = 0.91$, $p < 0.0001$).

Duration of phase 1 decomposition and characteristics of end product

We estimated the end of the period over which the mass loss and nitrogen dynamic patterns described above hold by taking the mean value for mass remaining for all data points beyond those used for the mass loss and inverse-linear calculations (e.g., Fig. 1A). Results again showed very little variation (Table 2) for those litter types that reached this end point (i.e., excluding fine root litter types and hemlock needles, $n = 11$, mean = 20.8 SEM = 1.73).

We can use initial N concentration, the slope of the inverse-linear relationship, and the mass remaining at the end of phase 1 to predict the N concentration at the end of this phase of decay. We can also use either the litter-specific or generalized exponential model to predict the time required to complete this phase. Alternatively, we can use the carbon fraction model to predict both time required to complete phase 1 and the carbon fraction chemistry at the end of this phase.

The slope of the inverse linear equation is

$$[2] \quad \text{slope} = \frac{\Delta MR}{\Delta \%N}$$

where ΔMR is 100 minus percentage of original mass remaining at the end of phase 1. Then

$$[3] \quad \Delta \%N = \frac{\Delta MR}{\text{slope}}$$

and

$$[4] \quad \text{final \%N} = \text{initial \%N} + \frac{\Delta MR}{\text{slope}}$$

Calculated values for %N at the end of phase 1 (Table 2) vary significantly between litter types mainly because of large differences in initial N concentration and small differences in slope. In contrast, predicted carbon fraction contents at the end of phase 1 are very similar for all litter types (Table 2; mean LCI = 0.050, SD = 0.0037).

Time required to reach the end of this phase can be estimated by each of the three methods used above to predict mass

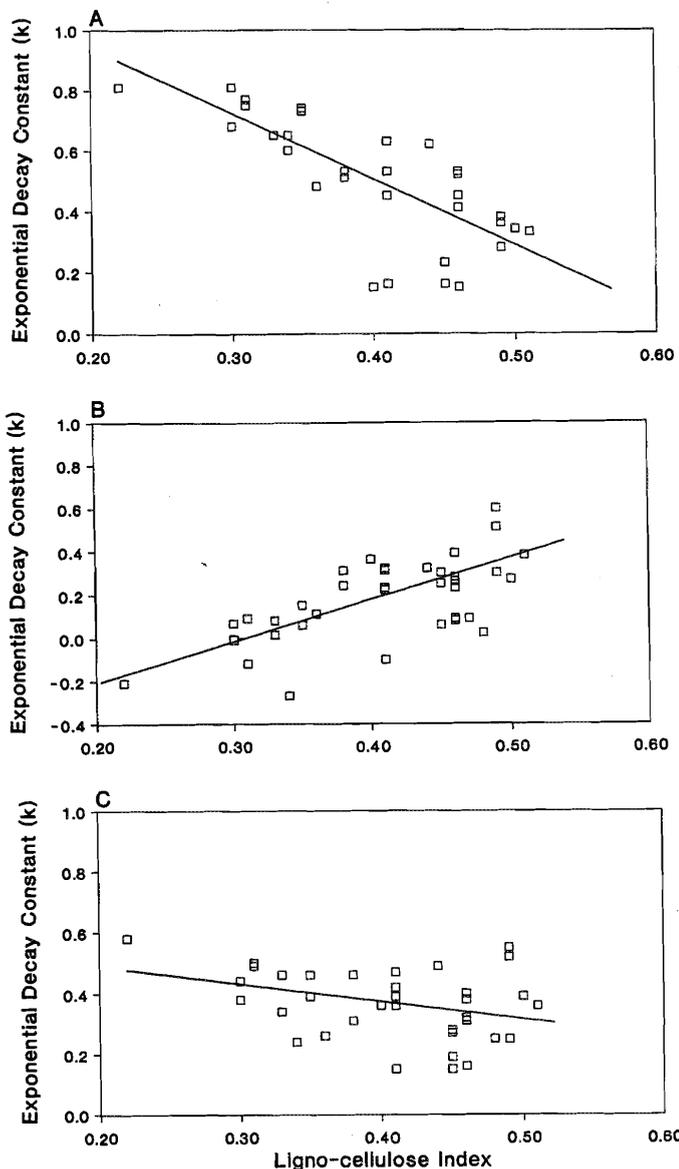


FIG. 3. Generalized decay rates of different carbon fractions as a function of the ligno-cellulose index (LCI = lignin/(lignin + cellulose)). (A) Extractives ($k = 1.346 - 2.119$ (LCI), $R^2 = 0.56$, $n = 35$, $p < 0.0001$). (B) Lignin ($k = -0.565 + 1.821$ (LCI), $R^2 = 0.46$, $n = 35$, $p < 0.0001$). (C) Cellulose ($k = 0.591 - 0.555$ (LCI), $R^2 = 0.12$, $n = 35$, $p < 0.02$).

loss (Table 2). Using litter-specific or generalized k values, the estimate is obtained by solving the exponential equation

$$[5] \quad y = e^{-kt}$$

for t , using $y = MR$, the mass remaining at the end of phase 1

$$[6] \quad \frac{\ln(MR)}{-k} = t$$

estimates from the carbon fraction model are determined by running the model with initial carbon fraction data until less than 20% of the original mass remains (the annual time step allows only an estimate of the year in which this end point is reached).

Actual time to the end of this phase, as determined statistically by the litter-specific exponential equations, ranges from

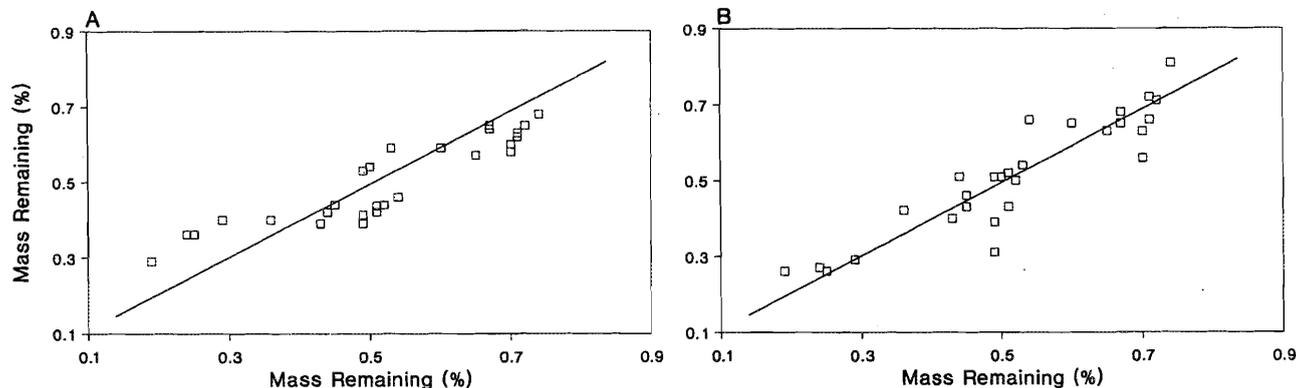


FIG. 4. Comparison of 1st and 2nd year predicted mass remaining values calculated from litter-specific exponential model (*x*-axis) with (A) carbon fraction model, and (B) generalized exponential model (see text for explanation of models).

2.3 to 7.9 years. Differences between these actual values and those predicted by the generalized exponential decay equation (GK in Table 2) are less than 1 year for all but two litter types. Data for hemlock needles, the outlier in Fig. 2, were not included in the regression equation, and therefore time to the end of phase 1 is poorly predicted from initial carbon fraction chemistry. The large error for sugar maple roots reflects the sensitivity of the estimate of time to the end of phase 1 to small errors in prediction of very low *k* values. The carbon fraction model, with the exception of sugar maple roots, predicts time to end of phase 1 to within a year of the actual time.

Discussion

Melillo et al. (1989) presented the concept of a "decay filter" that converts the wide variety of initial litter materials produced in forest ecosystems into chemically relatively uniform soil organic matter. The results reported here support this concept in that the carbon fraction chemistry does indeed become very uniform by the end of phase 1. However, there are very large differences in the nitrogen content of the material produced in this phase. This will have very important implications for future nitrogen cycling. We hypothesize that phase 2 organic matter will decay at relatively similar rates, regardless of origin, because of the similarity in carbon quality of phase 2 material produced from all fine litter types. Widely differing N concentrations will then result in very different rates of nitrogen mineralization. At very low N concentrations, this material could actually pass through a second immobilization phase as it is further processed to older, more stable, and more nitrogen-rich humus. While short-term N cycling rates may be affected by the phase 1 dynamics determined by initial carbon and nitrogen chemistry of litter material, long-term N cycling rates may be more affected by the N content of the material produced as an end product of phase 1 decay.

The abrupt shift in both mass loss and nitrogen dynamics that occurs at the end of phase 1 suggests that very different mechanisms are at work before and after this end point. Berg et al. (1982, 1984) separated an early period when cellulose, which is not physically shielded by lignin encrustations, is the major substrate for decay from a later period when lignin-shielded cellulose may be attacked but only with the coprocessing of lignin. However, the fact that the decay of the extractive fraction is also closely related to overall carbon quality of the material suggests that some degree of coprocessing

or shielding with lignin and cellulose occurs for this fraction as well. Berg and McClaugherty (1989) have shown that the initiation of lignin degradation and the net mineralization of nitrogen are also linked for many litter types.

The fact that lignin decay rate increases with increasing LCI and can be negative at low LCI may seem unlikely but is actually in keeping with decomposition theory. Humic precursors are thought to be produced by the transformation of compounds originally in litter and by synthesis from simpler secondary products of microbial metabolism. Many of these products are highly condensed substances that will fall into the acid-insoluble fraction in wet-chemistry digestion techniques.

Combining these factors, synthesis of acid-insoluble material would predominate in the early stages of decay and in lignin-poor material and would decline with decreasing litter quality, whereas lignin degradation would increase in lignin-rich (or acid-insoluble) material. Clearly the linear relationship in Fig. 3B cannot continue indefinitely. Lignin decay must decline rapidly in phase 2, as does mass loss in general. A nonlinear function in which lignin mass loss rate returns to zero as LCI approaches 0.5 would be a more logical form but could not be fit to the data available.

This analysis was in part a test of the generality of carbon fractions as indicators of litter quality and decay rate. The inclusion of both foliar and fine root data, with tissues from both evergreen conifers and deciduous broad-leaved species, was intended to push the limits of generalized predictions. With two exceptions, the derived generalized relationships held across tissue type and growth form. Those exceptions were (i) a lower decay rate for hemlock foliage litter than expected from initial carbon chemistry (Fig. 2), and (ii) more rapid than expected synthesis of acid-insoluble material in decaying fine root litters (Fig. 3B). Further research will be required to determine whether these result from the presence of compounds not detected by crude carbon fraction measurements (e.g., specific decay inhibitors) or from other characteristics that we did not measure. Further testing of these generalized relationships using data from a wider range of litter types would be very valuable.

Given the results of previous studies on factors controlling litter decay, it is not surprising that mass loss could be described well with an exponential equation or that the *k* parameter of that equation was highly correlated with initial lignin plus cellulose content. What was perhaps surprising is the relative uniformity of mass remaining and carbon fraction

concentrations at the end of phase 1. This analysis suggests that functional differences in types of humus formed under different species, to the extent that they occur, should relate to differences in nitrogen content of the material or in some other chemical characteristic that we have not measured.

Conclusions

Our results suggest that modeling of the organic matter and nitrogen dynamics of fine litter decay (excluding wood) in forest ecosystems can be accomplished accurately and with differing degrees of complexity, depending on the needs of the model and the data available. We can describe four levels of data intensity and prediction complexity to which the results in this paper would apply.

1. With a complete set of time series decay data for all litter types that continues through to the end of phase 1, a model can be constructed using the exponential decay constant (k) fit to each litter type and the inverse-linear relationship to calculate N dynamics. This will work for any time step.

2. If the litter decay data sets are not long enough to reach the end of phase 1, it is still accurate to fit the exponential and inverse-linear relationships and then to assume that these hold until 20% of initial mass remains.

3. If only initial carbon-fraction and nitrogen data are available for certain litter types, then k and the slope of the inverse-linear relationship can be predicted from these values and the functions extrapolated to 20% of original mass remaining.

4. If predictions of changes in carbon fractions are desired, then the relationships in Fig. 3 can be used. However, as this is the first time that relationships of this type have been derived, their generality may be questionable. The exponential and inverse-linear forms have a richer history to support them.

Predictions of decay rates generated by these techniques are applicable only to humid forested regions with similar climates. Other studies that relate decay to climatic variables (e.g., Meentemeyer 1978; Meentemeyer and Berg 1986) might be used to extrapolate the exponential decay models to different regions. A large regional-scale decomposition experiment to test the generality of these results and to develop relationships that include climatic drivers and so hold over large geographic regions should be a high priority. Such a study should include as wide a range of initial chemical quality as possible.

Acknowledgements

This research was supported by the U.S. National Science Foundation (grants BSR-8317531 and BSR-8718426). Andrea Ricca performed the carbon-fraction chemistry analyses.

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