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# Experimental Decomposition of Litter from the Tamaulipan Cloud Forest: A Comparison of Four Simple Models<sup>1</sup>

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## ABSTRACT

Four differential equation decomposition models were postulated, based on different assumptions of the behavior of the decomposition rate ( $\frac{1}{X} \cdot \frac{dX}{dt}$ ): Model 1, rate constant; Model 2, rate decreasing linearly as a function of the remaining litter fraction; Model 3, rate decreasing nonlinearly as a function of the remaining litter fraction; and Model 4, litter formed by two fractions, each having a constant decomposition rate but varying in proportion with time (thus the overall rate will also vary with time).

The models were tested against dry-weight data from three contrasting litter types from the Tamaulipan cloud forest: leaves of *Liquidambar styraciflua*, fruits of *Prunus serotina*, and branch segments of *L. styraciflua*. All three types were incubated in litter bags at constant temperature (30°C) and 100 percent relative humidity. Subsets of four replicates were collected, dry-weighed, and discarded at increasing intervals for three months.

Model 1 (the negative exponential) consistently gave the worst fit to the data. The best fits were obtained from Models 3 and 4, showing the high intrinsic heterogeneity of litter and, consequently, the variability of the relative decomposition rates.

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## RESUMEN

Sobre la base de diferentes supuestos respecto del comportamiento de la tasa intrínseca de descomposición ( $\frac{1}{X} \cdot \frac{dX}{dt}$ ), cuatro modelos de ecuaciones diferenciales fueron postulados: Modelo 1, tasa constante; Modelo 2, tasa linealmente decreciente en proporción a la fracción de mantillo remanente; Modelo 3, tasa no-linealmente decreciente; y Modelo 4, mantillo formado por dos fracciones cada una de ellas con tasa de descomposición constante pero diferentes entre sí (dado que las proporciones de cada fracción varían en el tiempo, la tasa global disminuye también con el tiempo).

Los cuatro modelos fueron probados contra datos de masa seca provenientes de tres tipos de residuos vegetales contrastantes colectados en el bosque mesófilo de Tamaulipas: hojas de *Liquidambar styraciflua*, frutos de *Prunus serotina*, y segmentos de ramas de *Liquidambar styraciflua*. Los tres tipos de material fueron incubados en bolsas de malla a temperatura constante (30°C) y 100 por ciento de humedad relativa. Durante tres meses, subconjuntos de cuatro réplicas fueron colectados a intervalos crecientes, secados y finalmente pesados.

El Modelo 1 (exponencial negativo) produjo consistentemente los peores ajustes a los datos. Los mejores ajustes fueron obtenidos por los Modelos 3 y 4, lo que muestra la alta heterogeneidad intrínseca del mantillo y la tendencia de la tasa intrínseca de descomposición a disminuir a medida que avanza la descomposición del material vegetal.

THE UNDERSTANDING OF DECOMPOSITION is often simplified by describing the process quantitatively as a whole, accounting for neither the interactions between organisms nor the individual results of each successive step. This approach has been the basis for the development of a series of mathematical models that represent decomposition in a simplified form, ignoring the highly heterogeneous biota that intervenes in the process and the great complexity of their interactions (Swift *et al.* 1979). These models are valuable in that they not only objectively describe the process, but also permit exploring and testing certain hypotheses about the functioning of the system (Bunnell 1973, Swift *et al.* 1979).

The equation most widely used to simulate decom-

position is the negative exponential developed by Jenny *et al.* (1949; for a detailed discussion see Olson 1963). This model is simple and functionally identical to the model of disintegration of radioactive isotopes. Both are based on the assumption that the proportion of material that is lost per unit time is constant. This appears to fit observations of the weight loss of litter in some cases (Satchell 1974), but in many others the results observed are different from those predicted by the exponential function (Minderman 1968, Bernhard-Reversat 1972, Angel & Wicklow 1974, Ewel 1976, Edwards 1977, Carpenter 1982). Recently, other models have been formulated as alternatives for describing decomposition as a function of time: ordinary differential equations have been formulated by Bunnell and Tait (1974), Carpenter (1982), Howard and Howard (1974), and Wieder and Lang (1982), and life tables have been proposed by Christian (1984). How-

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ever, some of these mathematical relations are complex, and others are based on questionable or unrealistic biological assumptions (Lousier & Parkinson 1976, Bunnell *et al.* 1977, Wieder & Lang 1982). Most decomposition studies reported in the literature were made under field conditions, where the process is influenced simultaneously by two uncontrolled environmental variables, moisture and temperature. Because environmental conditions are not constant, the lack of fit of a particular model can easily be attributable to changes in either of these two variables during the field study. Hence, experimental decomposition studies under controlled environmental conditions are needed.

This paper analyzes the theoretical propositions and performances of four differential equation decomposition models. The models are compared with controlled experimental data from three different types of litter collected in the Tamaulipan cloud forest. The equations are based on four simple and parsimonious (*i.e.*, having the minimum number of parameters) assumptions with regard to the mathematical behavior of the decomposition rate as a function of the remaining litter fraction at any given time. The theoretical predictions of the models are compared with annual litter production and standing-litter values in the cloud forest.

## METHODS

**SAMPLING PROCEDURE AND INCUBATION.**—Three different types of litter were collected from a cloud forest located in the wet eastern slope of the Eastern Sierra Madre, at the Rancho del Cielo, Tamaulipas, Mexico. The dominant species in this forest is *L. styraciflua* L., usually growing in association with *Quercus sartorii* Liebm., *Q. germana* Cham. et Schlecht., and *Clethra pringlei* Wats. A detailed floristic and phytogeographic description of the area is presented in Puig *et al.* (1983). Note that, although this forest occurs in a frost-free tropical region and is usually classified as a tropical forest, most of the overstory-dominant species have temperate affinities (Puig 1976).

Recently shed leaves of *L. styraciflua*, branch segments (approx. 4 cm long and 0.4–0.8 cm thick) from the same species, and fruits of *P. serotina* Ehr. were collected from the top layer of the ground litter. For each litter type, 32 litter bags (8 cm × 8 cm; mesh size 1.3 mm) were prepared, each bag containing 5 g air-dried material. The seeds within the *P. serotina* fruits were crushed to prevent germination and to allow decomposers to invade the seed substrate.

The bags were placed in an incubator at 30°C (±1°C) and 100 percent relative humidity, following a random block design on trays containing 10 cm of topsoil from the same forest. The soil acted as an incubation medium and as a source of microorganisms. Four randomly chosen bags (one bag per block) of each litter type were collected

at weekly intervals for the first three weeks, and every two weeks thereafter. The collected material was oven-dried at 85°C, weighed, and discarded. The initial ( $t = 0$ ) oven-dry mass of the samples was estimated from four additional 5-g replicates of each litter type, which were not incubated. The experiment was continued for 13 wk.

**MODELS USED AND ASSUMPTIONS INVOLVED.**—The four mathematical models postulated start from differential equations describing the behavior of the relative rate of decomposition (*i.e.*, the rate of decomposition per unit mass of litter).

**Model 1.**—This model assumes that the relative rate of decomposition is constant with time. Hence,

$$\frac{1}{X} \cdot \frac{dX}{dt} = -k \quad (1)$$

where  $X$  is the amount of litter at time  $t$ , and  $-k$  is the constant rate. Integrating Eq. (1) the model becomes

$$X_t = X_0 \exp(-kt) \quad (2)$$

where  $X_0$  is the initial ( $t = 0$ ) amount of litter. Eq. (2) represents the classical negative exponential model first proposed by Jenny *et al.* (1949).

**Model 2.**—In this case it is assumed that the decomposition rate decreases with time, as the more refractory fractions concentrate in the remaining litter. The simplest possible assumption is that the rate decreases as a linear function of the remaining fraction. Hence,

$$\frac{1}{X} \cdot \frac{dX}{dt} = -k(X/X_0) \quad (3)$$

where  $k$  is the initial decomposition rate, which will decrease as the remaining litter ( $X/X_0$ , containing the more refractory fractions) concentrates. Integrating Eq. (3) we obtain

$$X_t = \frac{X_0}{1 + kt} \quad (4)$$

which, like Model 1, is also a one-parameter model.

**Model 3.**—This model also assumes that the rate of decomposition decreases with the remaining fraction, but also assumes that it may do so in a nonlinear way. Thus,

$$\frac{1}{X} \cdot \frac{dX}{dt} = -k(X/X_0)^b \quad (5)$$

where  $b$  is a shape parameter. If the litter is rich in relatively labile compounds, then  $b < 1$ , and the rate will not decrease much as the first fractions are decomposed but will decrease considerably as the last fractions disintegrate. If the litter is rich in recalcitrant compounds, then  $b > 1$ , and the initial rate  $k$  will decrease more strongly as the first fractions decompose. If  $b = 1$ , the rate decreases linearly with the remaining fractions as in Model 2.

Integrating Eq. (5) we obtain the two-parameter model:

$$X_t = \frac{X_0}{(1 + bkt)^{1/b}} \quad (6)$$

If  $b = 1$ , Model 3 (Eq. 6) becomes Model 2 (Eq. 4). It can also be shown that for the limiting case  $b = 0$ , Model 3 simplifies to Model 1. A similar approach has been used by Godshalk and Wetzel (1978), who obtained good fits to decomposition data from a model that assumed the relative decomposition rate to be a negative exponential function of time  $\left(\frac{1}{X} \cdot \frac{dX}{dt} = k^{-bt}\right)$ .

Model 4.—For this model it is assumed that the total litter ( $X$ ) can be divided into two compartments, one labile and one refractory. A constant rate is assumed for each compartment (but, obviously, the overall rate will not be constant, as the proportion of the two fractions changes continuously with time). If we define  $p$  as the proportion of labile compounds initially present in the litter, then the final three-parameter model becomes

$$X_t = X_0(p \exp(-k_1 t) + (1 - p)\exp(-k_2 t)). \quad (7)$$

A detailed presentation of this model can be found in Bunnell and Tait (1974) and Hunt (1977). The overall decomposition rate can be calculated as function of time:

$$\frac{1}{X} \cdot \frac{dX}{dt} = \frac{-(k_1 p \exp(-k_1 t) + k_2(1 - p)\exp(-k_2 t))}{p \exp(-k_1 t) + (1 - p)\exp(-k_2 t)}. \quad (8)$$

FITTING THE EQUATION.—Each model was fitted numerically using a Hooke and Jeeves direct-search procedure (Himmelblau 1972) to estimate the least-squares values of the parameters which minimized the total error function  $TE = \sum_i \sum_j (X_{ij} - X_{pj})^2$ , where  $X_{ij}$  is the mass of litter remaining in bag  $i$  at time  $t_j$ , and  $X_{pj}$  is the mass of litter predicted by the model at time  $t_j$ .

The lack of fit of the model to the data, quantified as total error ( $TE$ ; *i.e.*, the sum of the squared residuals) can be partitioned into two components, a pure error ( $PE$ ) term and a regression error ( $RE$ ) term (Draper & Smith 1981). Pure error derives from the dispersion of the dependent variable ( $X$ ) for given values of the independent variable ( $t$ ), and it can be estimated for each period as the sum of the squared differences between each observation and the mean of all the observations for that particular time period ( $\bar{X}_t$ ). Hence  $PE = \sum_i \sum_j (X_{ij} - \bar{X}_t)^2$ . The pure error term has  $\sum_i (n_i - 1)$  degrees of freedom, where  $n_i$  is the number of observations at time interval  $t$ .

The error due to regression ( $RE$ ) derives from the failure of the model to describe the particular data set. It is calculated as the difference between  $TE$  and  $PE$ , and

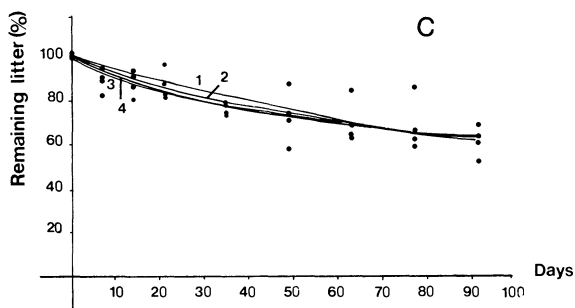
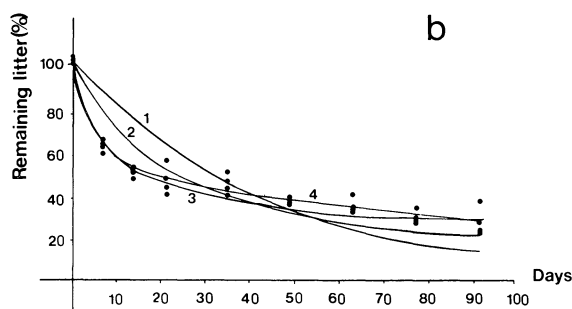
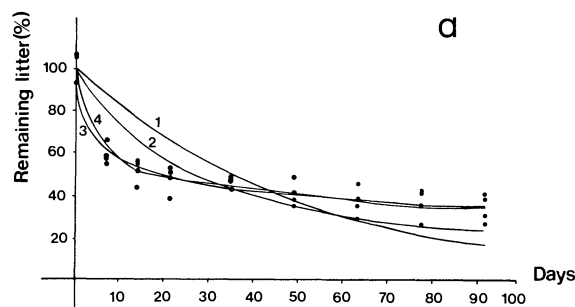


FIGURE 1. Changes in litter mass over time for (a) *Liquidambar* leaves, (b) *Prunus* fruits, and (c) *Liquidambar* branches. The continuous lines show the fitted curves for Models 1, 2, 3, and 4.

has  $r - q$  degrees of freedom, where  $r$  is the number of time intervals and  $q$  is the number of parameters in the model.

An  $F$  ratio (mean square of  $RE$ /mean square of  $PE$ ) can be used to test the null hypothesis that the error

TABLE 1. Probabilities for the variance ratio (F) test of regression error mean square against pure error mean square (PE/RE). The null hypothesis for this test implies that the fit is acceptable (see text); hence, the higher the probabilities, the better the fit. Asterisks indicate that the null hypothesis is rejected, i.e., that the model is not acceptable.

	Litter type		
	Leaves	Branches	Fruits
Model 1	<0.0001*	0.50	<0.0001*
Model 2	<0.0001*	0.79	<0.0001*
Model 3	0.95	0.90	0.17
Model 4	0.98	0.87	0.71

introduced by fitting the model is not significantly different from the internal (*i.e.*, within time-periods) variability of the data. If the null hypothesis is accepted, it is concluded that most of the total error is caused by random variation inherent to the data and that the fit is good. If the null hypothesis is rejected, it is concluded that the error introduced by fitting the model is unacceptably high and that the fit is not adequate. Although the *F* ratio test is not always strictly applicable because some parameters are frequently nonlinear, it can be used as an approximate value and as a measure of comparison between models (Draper & Smith 1981).

## RESULTS

THE PROGRESS OF DECOMPOSITION.—An analysis of variance on the dry masses showed highly significant differences between the three litter types ( $P < 0.0001$ ) and between the different harvest times ( $P < 0.0001$ ). Differences between blocks and interaction terms were all nonsignificant ( $P \gg 0.1$ ). As expected, decomposition was faster for the softer litter types (leaves and fruits) and slower for the more lignified branches (Fig. 1). Additionally, branches presented a higher variability in dry mass (indicated by a high *PE* value when fitting the models), possibly because of a higher heterogeneity in both size and chemical composition of this litter type, or because of varying initial degrees of invasion by microorganisms for the different branch fragments.

All four models described the decomposition of

branches (woody parts) in an acceptable manner, but in the case of the softer litter classes (leaves and fruits), only Models 3 and 4 adequately described the decomposition process (Fig. 1, Tables 1 and 2). In all cases, the worst fit was obtained with the negative exponential model. Model 4 gave the best descriptions of the decomposition of fruits, probably because this litter type fits best the two-compartment assumption. In effect, *P. serotina* fruits consist of two principal fractions: the pericarp (composed chiefly of a soft and fleshy mesocarp) and the seed (composed mostly of the endosperm).

ESTIMATING THE DECOMPOSITION RATES.—An adequate knowledge of how relative decomposition rates change as the process advances is central to selecting a good decomposition model. It is a standard result from calculus that  $\frac{d \cdot \ln \cdot X}{dX} = \frac{1}{X}$ . Therefore, the differential expression for the rate can be rewritten as

$$\frac{1}{X} \cdot \frac{dX}{dt} = \frac{d \cdot \ln \cdot X}{dt} \quad (9)$$

Hence,

$$\frac{1}{X} \cdot \frac{dX}{dt} \approx \Delta \ln X_i / \Delta t \quad (10)$$

Using Eq. (10), the rate for any given time interval can be estimated. These rates can be plotted as a function of the remaining fraction ( $X_t/X_0$ ) during the same interval. The value  $X_t$  (fraction remaining at the middle of the time interval) can be estimated from Eq. (9):

$$X_t = dX / d \cdot \ln \cdot X \approx \Delta X_t / \Delta \ln \cdot X \quad (11)$$

Figure 2 shows the estimated average rates (one for each time interval) as a function of the remaining litter fractions, and the curves predicted by the different models. For Models 1, 2, and 3, these functions were obtained directly from Eqs. (1), (3), and (5), respectively, with the estimated parameters shown in Table 2. For Model 4 the rate cannot be calculated as a direct function of the remaining fraction, but both rate and remaining fraction can be simultaneously derived as a function of time from Eqs. (7) and (8), thus forming an implicit functional relationship.

TABLE 2. Least-squares estimates of the parameters for the four models.

Litter type	Model 1	Model 2	Model 3		Model 4		
	<i>k</i>	<i>k</i>	<i>k</i>	<i>b</i>	<i>p</i>	<i>k</i> <sub>1</sub>	<i>k</i> <sub>2</sub>
Leaves	0.0197	0.0374	0.2680	4.550	0.4438	0.2627	0.0057
Fruits	0.0235	0.0462	0.1694	3.218	0.4718	0.2153	0.0072
Branches	0.0057	0.0070	0.0105	3.003	0.1150	0.0748	0.0038

As can be observed in Figure 2, decomposition did not occur at a constant rate, but rather the rates tended to decrease as a function of the remaining litter fraction. In the case of branches this pattern was not so clear, possibly because of the extremely high variability in the data. In all cases, however, the decomposition rate during the first week of incubation was much higher than during the rest of the experiment.

LITTER ACCUMULATION ON THE GROUND.—If  $X_0$  is the average amount of litter that falls from the canopy per day, then

$$L_z = \int_0^z X_t dt. \quad (12)$$

represents the amount of organic matter that will accumulate in the system after  $z$  days. This integral can be solved analytically for all four models, yielding the following accumulation functions:

$$\text{Model 1: } L_t = \frac{X_0}{k} \cdot [1 - \exp(-kt)] \quad (13)$$

$$\text{Model 2: } L_t = \frac{X_0}{k} \cdot \ln(1 + kt) \quad (14)$$

$$\text{Model 3: } L_t = \frac{X_0}{k} \cdot \frac{1}{(b-1)} \cdot \left[ \frac{1 + bkt}{(1 + bkt)^{1/b}} - 1 \right] \quad (15)$$

$$\text{Model 4: } L_t = X_0 \cdot \left\{ \frac{p}{k_1} [1 - \exp(-k_1 t)] + \frac{(1-p)}{k_2} [1 - \exp(-k_2 t)] \right\} \quad (16)$$

where, again, it can be proven that Models 1 and 2 are the limiting cases for Model 3 when  $b \rightarrow 0$  and  $b \rightarrow 1$ , respectively. The amount of litter on the ground when steady-state conditions are obtained can be estimated as

$$L_{ss} = \lim_{t \rightarrow \infty} L_t. \quad (17)$$

For Model 1, this limit is  $L_{ss} = X_0/k$ . Model 2 does not have a limit, though the slope of the accumulation function (Eq. 14) decreases monotonically with time. This model predicts that the more refractory fractions of the litter will tend to accumulate on the soil surface. Model 3 has an equilibrium state

$$L_{ss} = \frac{X_0}{k} \cdot \left( \frac{1}{1-b} \right) \quad (18)$$

only if  $b < 1$ . If  $b > 1$  the model predicts a similar behavior as Model 2: organic matter will accumulate in the system at an ever-decreasing rate. The first derivative with respect to time of Eqs. (14) and (15) is positive, whereas the second one is negative for  $0 \leq t < \infty$ . Model

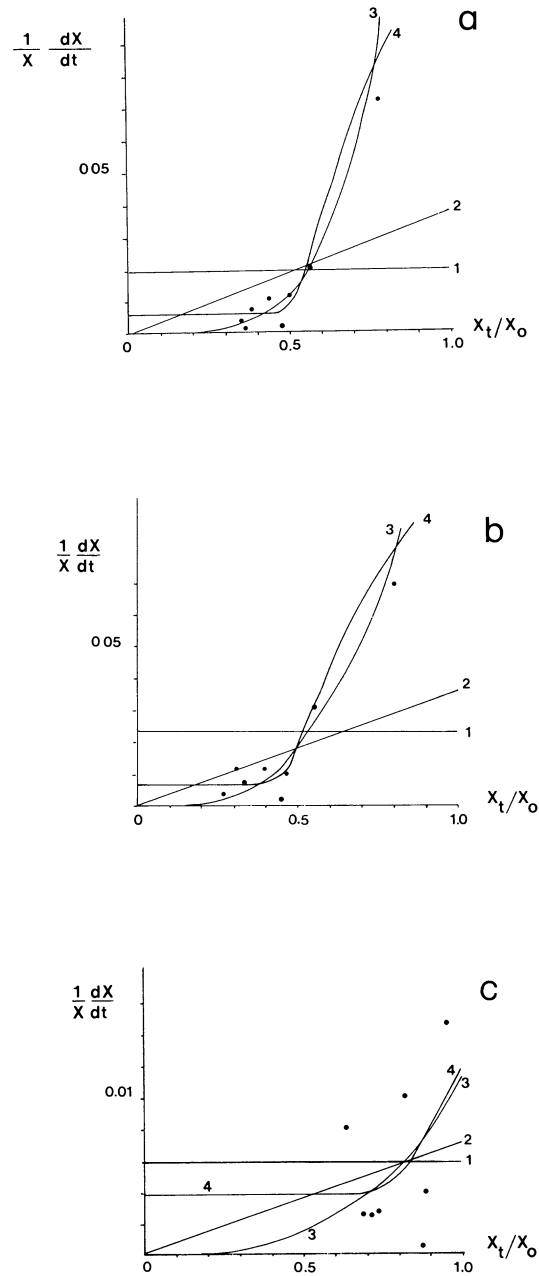


FIGURE 2. Estimated relative decomposition rates as a function of the remaining litter fraction ( $x_t/x_0$ ) for (a) *Liquidambar* leaves, (b) *Prunus* fruits, and (c) *Liquidambar* branches. The continuous lines show the expected curves derived from Models 1, 2, 3, and 4.

TABLE 3. Litter accumulation on the forest floor predicted by the four models.

Time (yr)	Forest floor litter mass (kg/m <sup>2</sup> )			
	Model 1	Model 2	Model 3	Model 4
1	0.10	0.14	0.24	0.17
10	0.10	0.26	1.51	0.19
100	0.10	0.39	8.90	0.20
500	0.10	0.47	31.24	0.20

4, like Model 1, always predicts an equilibrium no matter what values the parameters take. In this case,

$$L_{ss} = X_0 \left( \frac{b}{k_1} + \frac{1-p}{k_2} \right). \quad (19)$$

The three types of litter used in this study were obtained from a forest dominated by *L. styraciflua* and in which the rate of litter input to the forest is about 2 g/m<sup>2</sup> day (Puig *et al.* 1983, pers. comm.). Using this litter input value and the parameters describing the decomposition of *Liquidambar* leaves (Table 2), the accumulation of litter on the forest floor over time can be roughly predicted (Table 3).

The standing litter in this *Liquidambar*-dominated forest is somewhat less than 1 kg/m<sup>2</sup> (R. Bracho, V. Sosa, & H. Puig, pers. comm.), whereas the total organic matter (*i.e.*, above-ground litter plus organic matter in the soil profile) is approximately 40 kg/m (considering an A horizon 0.20 m thick, with bulk density 1 g/cm<sup>3</sup> and 20% organic matter). It is clear that, whereas Model 4 predicts an accumulation value near (within an order of magnitude) the above-ground litter value, Model 3 predicts an accumulation value 30 times higher than the standing litter in the field and still slowly increasing. The value predicted by Model 3, however, approaches the total organic matter on and within the soil.

It seems contradictory at first that two models which adequately describe the process of decomposition predict such different values of litter accumulation on the ground. The reasons for this can be seen in Figure 2 and in the theoretical assumptions of the respective models. Model 3 assumes that the decomposition rate will decrease as more of the original litter is decomposed, approaching zero as the more refractory portions become concentrated. In reality, these last litter fractions will disappear into the soil by fragmentation and leaching at a low but constant final rate, and will tend to accumulate within the profile as humic substances (note that more than 95% of soil organic matter is within the profile, and less than 5% forms the surface litter). Because Model 3 assumes that the final rate approaches zero, it erroneously predicts the above-ground accumulation of the more recalcitrant fractions. Model 4, on the other hand, assumes that the rate will decrease

until practically all the labile compartment has been decomposed. Then the remaining fraction (*i.e.*, the refractory material) will decompose at a constant final rate (Fig. 2). This assumption will tend to exclude the more refractory fractions, which are leached from the surface litter into the soil profile.

A differential equation model that includes both a nonlinear decrease in relative decomposition rate and a final constant litter disappearance rate can be postulated as  $\frac{1}{X} \cdot \frac{dX}{dt} = -[a + k(X/X_0)^b]$ , where  $a$  is the final rate,  $(a + k)$  is the initial ( $t = 0$ ) rate, and  $b$  is the shape parameter. Unfortunately, we have found no simple way to integrate this equation, which has to be solved numerically.

## DISCUSSION

Under laboratory conditions, the relative decomposition rates of the three litter types were not constant but progressively decreased over time as the more labile parts decomposed. Moreover, the decrease in relative decomposition rate as a function of the remaining litter fraction was strongly nonlinear. Both Model 1 (the negative exponential) and Model 2 were inadequate for describing litter decomposition under simulated field conditions. Model 3 (nonlinear decrease in relative decomposition rate) and Model 4 (two-compartment, or double exponential model) reflected the mass losses of the three different types of litter in an adequate manner.

Model 4 (the double exponential) accurately described the decomposition process. However, the division of litter into two compartments that are not chemically defined or measured may not be a realistic assumption. Minderman (1968) showed that the resistance to decomposition of the different litter compounds is highly variable. It seems, therefore, that there is little biological support for dividing organic matter into two unique fractions, each with a constant decomposition rate. The good fit of this model is probably due more to the higher number of parameters in Eq. (7) than to ecologically realistic assumptions.

With only two parameters, Model 3 provides a flexible and accurate relation. The shape parameter ( $b$ ) confers a nonlinear change in the relative decomposition rate and represents the effect of the resource quality on the decomposition process. This model is a simple alternative for describing the mass losses of decomposing litter through time.

Single-parameter models often fail to adequately describe decomposition data. There is clearly a tradeoff between the simplicity of the model and the accuracy of its predictions. Adding additional parameters almost always improves the fit, but these increasingly complex models become less and less parsimonious.

According to Levins (1968), a model is built by a process of abstraction (*i.e.*, postulating hypothesis) that defines a set of sufficient parameters on the level of study, and a process of simplification that is intended to leave intact the essential aspects of reality while removing distracting elements. Hence, when fitting these different models, we are in effect testing different hypotheses with regard to the nature of the decomposition process. (It is interesting to note in this sense that the double exponential model gave a markedly better fit only on the *Prunus* fruits, where the two-compartment assumption is more plausible.) Every model can be considered a sample from a universe of possible models, differing from the rest in its degree of realism, precision, and generality. Maximizing

one of these properties usually implies sacrificing another (Levins 1968). There is probably no such thing as the "best" decomposition model but, rather, different models with different underlying assumptions which can be tested by analyzing the fit of the model to the data.

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