

Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison

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Abstract

Decomposition is a critical process in global carbon cycling. During decomposition, leaf and fine root litter may undergo a later, relatively slow phase; past long-term experiments indicate this phase occurs, but whether it is a general phenomenon has not been examined. Data from Long-term Intersite Decomposition Experiment Team, representing 27 sites and nine litter types (for a total of 234 cases) was used to test the frequency of this later, slow phase of decomposition. Litter mass remaining after up to 10 years of decomposition was fit to models that included (dual exponential and asymptotic) or excluded (single exponential) a slow phase. The resultant regression equations were evaluated for goodness of fit as well as biological realism. Regression analysis indicated that while the dual exponential and asymptotic models statistically and biologically fit more of the litter type–site combinations than the single exponential model, the latter was biologically reasonable for 27–65% of the cases depending on the test used. This implies that a slow phase is common, but not universal. Moreover, estimates of the decomposition rate of the slowly decomposing component averaged $0.139\text{--}0.221\text{ year}^{-1}$ (depending on method), higher than generally observed for mineral soil organic matter, but one-third of the faster phase of litter decomposition. Thus, this material may be slower than the earlier phases of litter decomposition, but not as slow as mineral soil organic matter. Comparison of the long-term integrated decomposition rate (which included all phases of decomposition) to that for the first year of decomposition indicated the former was on average 75% that of the latter, consistent with the presence of a slow phase of decomposition. These results indicate that the global store of litter estimated using short-term decomposition rates would be underestimated by at least one-third.

Keywords: decay, decomposition, fine roots, leaves, litter, long-term study, rate constant, stable fraction

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Introduction

Plant litter in the form of dead leaves and roots is a source of soil organic matter, the largest terrestrial store of carbon (Post *et al.*, 1982). The current size of this store

and its fate under global environmental change requires insight into the long-term temporal pattern of litter decomposition (Kirschbaum, 2000). Little is known about long-term patterns of decomposition, in part, because few experiments have tracked the process from fresh litter to the formation of highly decomposed material. Nearly 4000 papers have been published on the topic of litter decomposition (Institute of Scientific Information Web of Science), but few extend beyond a

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¹See Table 1 for the list of 27 LIDET team members

given ecosystem type for more than several years (e.g. Gholz *et al.*, 2000; Trofymow *et al.*, 2002). The vast majority of experiments have lasted 1–2 years (Swift *et al.*, 1979; Melillo *et al.*, 1984; Vogt *et al.*, 1986; Silver & Miya, 2001) yielding many insights into the temporal pattern early in decomposition (Olson, 1963; Howard & Howard, 1974) as well as the controls on initial mass loss such as initial litter quality (Minderman, 1968; Bunnell & Tait, 1977; Fogel & Cromack, 1977; Melillo *et al.*, 1982), invertebrates (Kurcheva, 1960; Witkamp & Olson, 1963; Witkamp & Crossley, 1966), and environmental variables such as temperature and moisture (Bunnell *et al.*, 1977; Meentemeyer, 1978; Jansson & Berg, 1985; Yahdjian *et al.*, 2006). However, 2 years is not enough time in most environments to reveal dynamics in the later phases of this key ecosystem process.

Previous investigators have proposed conceptual models of decomposition with at least two distinct phases, although ideas have differed on the mechanisms distinguishing the phases and the degree of recalcitrance or stability of material in the later phases. Coûteaux *et al.* (1995) proposed a two-phase conceptual model in which Phase I was dominated by the loss of soluble and relatively labile compounds from litter, including some of the cellulose present. In Phase II, decomposition continued, but with a strong control exerted by lignin. In contrast, Melillo *et al.* (1989) and Aber *et al.* (1990) proposed a two-phase conceptual model in which the material in Phase II was similar, if not identical to soil organic matter and was termed 'stable' over a time-span of approximately a decade.

The gradually slowing absolute rate of mass loss from decaying litter over time can be captured by a first-order or exponential decay function [Eqn (1)] where M_t is litter mass at time t , M_0 is initial litter mass, and k is the rate constant of loss

$$M_t = M_0 e^{-kt}, \quad (1)$$

However, the long-term studies (e.g. Aber *et al.*, 1990; Magill & Aber, 1998; Berg *et al.*, 2001; Trofymow *et al.*, 2002; Moore *et al.*, 2005) that have been conducted suggest that in later stages rates of decomposition slow to a degree beyond that captured by a single-exponential decomposition curve. For litters high in soluble and labile fractions, a very rapid phase of decomposition may also occur within days to weeks of litter formation (Harmon *et al.*, 1990; Currie & Aber, 1997). Exponential rate constants of mass loss (i.e. the proportion lost per unit time) of the soluble and labile fractions during this phase may exceed 10 year^{-1} , indicating this material is lost within a few months. During the following phase, which dominates the first few years for many litter types in temperate environments, structural polymers are degraded. While there is considerable range in the

speed at which these materials are degraded, exponential rate constants of $0.1\text{--}5 \text{ year}^{-1}$ are typical (Singh & Gupta, 1977; Swift *et al.*, 1979; Vogt *et al.*, 1986). As these polymers are degraded, residual and newly formed recalcitrant materials begin to dominate the decomposition process. The size and rate this late phase pool decomposes are not well established and may have a great deal of variability (Berg & McClaugherty, 2003). In some cases, slow phase decomposition rates appear to be very low (Berg *et al.*, 1984). Carbon isotope studies suggest that rate constants for highly decomposed soil organic matter, i.e. material that is generally complexed with mineral material, are typically below 0.01 year^{-1} (Gaudinski *et al.*, 2000; Trumbore, 2000). Modeling analysis of the forest floor in northern hardwoods forests of the northeastern United States suggests that if Phase II *sensu* Aber *et al.* (1990), starts when 20% of the original litter mass remained, then a rate constant of 0.017 year^{-1} would be needed to match the measured forest floor mass (Currie & Aber, 1997).

A major gap to studying decomposition is the lack of a careful assessment of the philosophy supporting and consequences of choosing certain mathematical models describing the course of decomposition. The single negative exponential model [Eqn (1)] has been most commonly used to determine the decomposition rate of litter. This model often does not capture the initial very rapid loss phase adequately (Blair *et al.*, 1990; Chen *et al.*, 2002), but has worked remarkably well for the majority of data from short-term experiments. If decomposition follows this simple exponential pattern, then predicting temporal patterns in the later stages of decomposition by extrapolation is possible. However, the long-term data that exist indicate a relatively slow phase of decomposition is eventually reached (Lousier & Parkinson, 1978, 1979; Berg *et al.*, 1984; Edmonds, 1984; McClaugherty *et al.*, 1985; Chen *et al.*, 2002) and sometimes an asymptote in mass being reached implying extremely slow decomposition (Wardle *et al.*, 1997; Berg *et al.*, 2001).

There are two alternatives to the single negative exponential equation: the multiple (or in the most simple case the dual) exponential; and the negative exponential with an asymptote (Howard & Howard, 1974; Wieder & Lang, 1982). Both equations capture the transition from rapid to slow decomposition, although the asymptotic equation implies a steady accumulation of partially decomposed litter (because the litter represented by the asymptote does not decompose). In addition to deriving separate decomposition rates for each of the multiple fractions (e.g. the 'fast' and 'slow' fractions), these equations require estimating the initial proportions of these fractions. Previous studies on hardwood species in the northeastern United States indi-

cated that approximately 20% of the initial litter was formed of slowly decomposing material (Aber *et al.*, 1990). Berg (2000a,b) found that it varied from 6% to 47% of initial forest litter mass, depending on the amount of nitrogen present. The degree this slowly decomposing fraction is initially present or created by the many biological and chemical reactions that we term 'decomposition' is still under debate. While some litter types apparently enter a phase in which decomposition rates are relatively low, it is unclear whether this is a general pattern; if so, the degree that it is influenced by substrate quality, environment, and their interactions needs to be elucidated.

This paper provides a general overview of Long-term Intersite Decomposition Experiment Team (LIDET), a study that generated a dataset that we use to test the generality of a late, slow phase of decomposition (Moorhead *et al.*, 1999; Gholz *et al.*, 2000). Our specific objectives in this paper are: (1) to examine a series of mathematical models to test how well they statistically fit observations and how well they conformed to biological expectations; (2) to evaluate the generality of a slow phase and the fraction of the litter involved; and (3) to provide estimates of how fast this material decomposed.

The LIDET study

Background

The data used in this study were from the LIDET, a project which carried out a 10-year field study with the primary objective of testing the degree to which substrate quality and climate control the long-term carbon and nitrogen dynamics of decomposing leaf and fine root litter (Table 1). LIDET employed a standardized methodology at a large number of sites (27) to examine decomposition patterns within the first decade of decomposition of 30 species of litter. In addition to characterizing the climate during the course of the experiments, the chemical nature of the material used in the experiment was described using a wide range of carbon fractions and nutrient elements. LIDET therefore represents one of the few comprehensive, long-term or large-scale datasets from which to develop generalizable patterns.

General experimental design

Three experiments were conducted by LIDET: (1) a comparison of long-term leaf and fine root decomposition to examine the effect of substrate quality and climate on patterns of long-term decomposition and nitrogen accumulation in above- and below-ground fine

litter, (2) a comparison of leaf decomposition with and without macroinvertebrates, and (3) a comparison of environmental influences on wood decomposition above- and below-ground using wooden dowels as a common substrate. The major factors considered in the leaf and fine root experiment, the focus of this paper, were site, species of litter, and time. There were 27 sites, representing a wide array of moisture and temperature conditions, at which the experiments were installed (Table 1, Fig. 1). Each site was characterized in terms of location (i.e. latitude and longitude), elevation, climate [precipitation, temperature, Actual Evapotranspiration (AET), potential evapotranspiration, Climate Decomposition Index (CDI); see Adair *et al.*, 2008], and vegetation (biome type and specific vegetation cover). The sites span a wide array of ecosystem types from tundra to warm desert to shortgrass steppe to moist tropical forest. Climate data were taken from measurements at the site or from nearby climatic stations. Precipitation ranged from 24 to 409 cm yr⁻¹ and mean annual air temperature ranged from -7 to 26 °C (Fig. 2). Nine types of 'standard' litters were sent to each of the 27 sites including: three types of fine roots (graminoid, hardwood, and conifer) and six types of leaf litter that ranged in AUF/nitrogen ratio from 5 to 50 (Table 2, Fig. 3). Samples were collected 10 times and there were four replicates for each species, site, and time. In addition to the standard litters, each site is represented by a 'wildcard' litter that appeared at one site for each sample collection. The purpose of the wildcard species was to verify the predictions from the standard species. There were also four replicates for each wildcard species, site, and time.

Materials and methods

Field and laboratory

Fresh leaf and fine roots for the standard litters was gathered from five of the 27 LIDET sites. The leaves were collected by a range of methods, ranging from collection of senescent leaves from trees (the primary method), to collecting freshly fallen litter from the ground, to removing green foliage (used at one of the tropical sites). Fine roots (<2 mm diameter) were collected by either excavating surface roots and washing or collecting material exposed along stream banks. All litter was air dried at room temperature before shipment to Oregon State University except materials those from Luquillo which were oven-dried at 50 °C to halt decomposition.

All the litterbags used were 20 cm × 20 cm and filled with an air-dried mass of 10 g leaves and 5–7 g of fine roots. Each bag was identified with a unique number

Table 1 General characteristics of sites used in the LIDET study and the list of LIDET team members

Site	Code	Latitude	Longitude	Biome type	MAP	MAT	AET	PET	Elev	LIDET team member
*H. J Andrews Experimental Forest, Oregon	AND	44°14'N	122°11'W	Temperate Conifer Forest	230.9	8.6	76.4	98.2	500	M. Harmon
*Arctic Lakes, Alaska	ARC	68°38'N	149°34'W	Tundra	32.7	-7.0	28.4	42.3	760	J Laundre
Barro Colorado Island, Panama	BCI	9°10'N	79°51'W	Humid Tropical Seasonal Forest	269.2	25.6	136.8	151.7	30	J. Wright
*Bonanza Creek Experimental Forest, Alaska	BNZ	64°45'N	148°00'W	Boreal Forest	40.3	-5.0	36.0	57.6	300	J. Yarie
Blodgett Research Forest, California	BSF	38°52'N	105°38'W	Temperate Conifer Forest	124.4	14.4	75.3	109.7	1300	S. Hart
*Cedar Creek Natural History Area, Minnesota	CDR	45°24'N	93°12'W	Temperate Woodland/Humid Grassland	82.3	5.5	73.3	102.6	230	D. Wedin
*Central Plains Experimental Range, Colorado	CPR	40°49'N	104°46'W	Temperate Shortgrass	44.0	8.9	43.0	120.2	1650	I. Burke
*Coweeta Hydrological Laboratory, North Carolina	CWT	35°00'N	83°30'W	Temperate Deciduous Forest	190.6	12.5	117.3	135.3	700	B. Clinton
Guanica State Forest, Puerto Rico	GSF	17°57'N	65°52'W	Dry Tropical Forest	50.8	26.3	50.2	142.2	80	A. Lugo
*Hubbard Brook Experimental Forest, New Hampshire	HBR	43°56'N	71°45'W	Temperate Deciduous Forest	139.6	5.0	71.2	81.7	300	T. Fahey
*Harvard Forest, Massachusetts	HFR	42°40'N	72°15'W	Temperate Deciduous Forest	115.2	7.1	85.1	104.1	335	J. Melillo
*Jornada Experimental Range, New Mexico	JRN	32°30'N	106°45'W	Warm Semi-desert	29.8	14.6	29.2	166.6	1410	J. Anderson
Juneau, Alaska	JUN	58°00'N	134°00'W	Temperate Conifer Forest	287.8	4.4	49.5	54.4	100	M. McClellan
*Kellogg Biological Station, Michigan	KBS	42°24'N	85°24'W	Agro Ecosystem	81.1	9.0	70.6	100.7	288	S. Halstead
*Konza Prairie Research Natural Area, Kansas	KNZ	39°05'N	96°35'W	Temperate Tallgrass	79.1	12.8	74.7	125.0	366	J. Blair
La Selva Biological Station, Costa Rica	LBS	10°00'N	83°00'W	Humid Tropical Forest	409.9	25.0	169.9	177.3	35	P. Sollins
*Luquillo Experimental Forest, Puerto Rico	LUQ	18°19'N	65°49'W	Humid Tropical Forest	336.3	23.0	123.4	125.9	350	J. Lodge
Loch Vale Watershed, Colorado	LVW	40°17'N	105°39'W	Boreal Forest	109.6	1.6	85.1	108.3	3160	J. Baron
Monte Verde, Costa Rica	MTV	10°18'N	84°48'W	Tropical Elfin Cloud Forest	268.5	17.7	108.4	116.6	1550	N. Nadkarni
North Inlet (Hobcaw Barony), South Carolina	NIN	33°30'N	79°13'W	Wetland	149.1	18.1	120.6	145.6	2	J. Morris
*North Temperate Lakes, Trout Lake Station, Wisconsin	NLK	46°00'N	89°40'W	Temperate Deciduous Forest	67.7	4.4	64.9	88.4	500	T. Gower

Continued

Table 1 Continued

Site	Code	Latitude	Longitude	Biome type	MAP	MAT	AET	PET	Elev	LIDET team member
*Niwot Ridge/Green Lakes Valley, Colorado	NWT	40°03'N	105°37'W	Tundra	124.9	-3.7	64.7	75.6	3650	J. Baron
Olympic National Park, Washington	OLY	47°50'N	122°53'W	Temperate Conifer Forest	153.1	10.0	79.4	104.4	150	R. Edmonds
*Seville National Wildlife Refuge, New Mexico	SEV	34°29'N	106°40'W	Warm Semi-desert	25.4	16.0	25.2	160.2	1572	C. White
Santa Margarita Ecological Reserve, California	SMR	33°30'N	117°45'W	Annual Grassland	24.0	16.4	23.6	186.0	500	P. Zedler
University of Florida, Florida	UFL	29°45'N	82°30'W	Temperate Conifer Forest	123.8	21.0	116.6	162.1	35	H. Gholz
*Virginia Coast Reserve, Virginia	VCR	37°30'N	75°40'W	Wetland	113.8	15.0	99.3	121.5	0	L. Blum

LIDET, Long-term Intersite Decomposition Experiment Team; MAP, mean annual precipitation (cm); MAT, mean annual temperature (°C); AET, actual evapotranspiration (cm); PET, potential evapotranspiration (cm); elev, elevation (m). Climatic data are for the duration of the experiment. Asterisks denote that the site is a member of the Long Term Ecological Research (LTER) network.

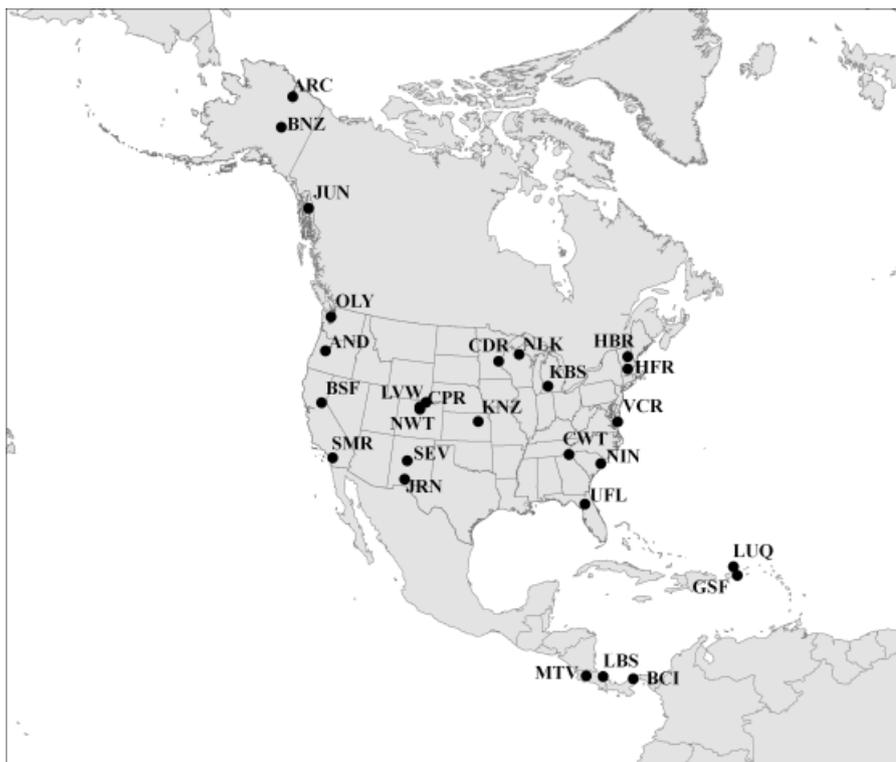


Fig. 1 Location of the Long-term Intersite Decomposition Experiment Team (LIDET) study sites.

embossed on an aluminum tag. The bag openings were sealed with six Monel staples. The initial air-dry weight, calculated oven-dry weight, species, site, and replicate number for each litterbag were recorded before placement in the field. Subsamples of litter material were taken to determine the air-dry to oven-dry conversion

factor and the initial chemistry of the litter. These were taken at the start and end of each weighing session, with an additional sample taken in the middle of longer sessions. The standard deviation of the air dried litter moisture content for all 120 samples was 2%, with a standard error of 0.002%. Two types of bags were used

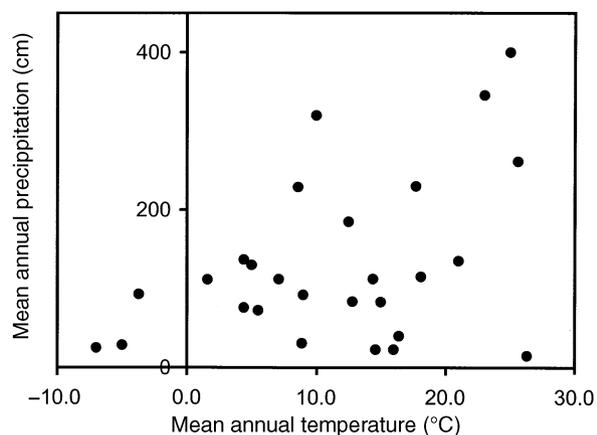


Fig. 2 Range of mean climate conditions for the sites used in Long-term Intersite Decomposition Experiment Team (LIDET).

in this experiment. For the long-term leaf litter experiment, the bags had a top mesh of 1 mm nylon and a bottom of 55 μ m Dacron. The bags used for fine roots were made entirely of 55 μ m Dacron mesh.

Samples were placed in the field during fall of 1990 or 1991 by each of the participating sites. Four separate locations at each site were selected to represent the range of typical conditions. At each of these locations, 10 sets of litter bags were placed. Each set of 10 bags to be collected at a given time and location were tethered to a cord; these sets of bags were laid out in parallel lines in a random order. Leaf litter bags were placed on the ground surface. Fine root bags were placed within the top 20 cm of the soil by cutting into the soil with a shovel at a 45° angle, sliding the root bag into the cut, and then firmly pressing the overlying soil onto the bag.

All sites, other than the tropical ones, collected the fine litter on an annual basis for a 10-year period. For tropical sites (Barro Colorado Island, La Selva, Luquillo, and Monteverde) sampling was conducted every 3–6 months. Once the litter or dowels were collected, the fresh and oven-dry weight was determined and recorded. Samples were oven dried in paper bags at 55 °C until the mass was stable. The samples were then sent to Oregon State University for preparation for chemical analysis as well as reweighing of selected samples for data quality checks. The contents of each litterbag were ground separately and stored in plastic vials labeled to identify the species, site, and time the sample was taken. Samples were also pooled by species, site, and time to provide samples for wet chemical and near infrared (NIR) analysis.

Nitrogen and carbon concentration was determined on a Leco C/N/S-2000 Macro Analyzer (Leco Inc, St Joseph, MI, USA). Ash concentration was determined by heating in a muffle furnace at 450 °C for 8 h. Analysis

of carbon fractions for undecomposed litter followed the methods of McClaugherty *et al.* (1985) and Ryan *et al.* (1990). Nonpolar extractives, (i.e. soluble fats, waxes, and oils) were removed using dichloromethane (Tappi, 1976; Bridson, 1985). Simple sugars and water soluble phenolics were removed with hot water (Tappi, 1981). Simple sugars were determined with the phenol-sulfuric acid assay (DuBois *et al.*, 1956). Water soluble phenolics were determined using the Folin-Denis procedure (Hagerman, 1988; Haslam, 1989). The acid unhydrolysable fraction, traditionally called lignin, was determined by hydrolyzing extractive-free material with sulfuric acid and weighing the residue (Effland, 1977; Obst & Kirk, 1988). Hydrolysates were analyzed for carbohydrate content using the phenol-sulfuric acid assay (DuBois *et al.*, 1956).

Mathematical models

The data used for this analysis were derived from the LIDET study (Moorhead *et al.*, 1999, Gholz *et al.*, 2000) and we only analyzed data for the 'standard litters' that were placed at all of the 27 sites for each sample time (the raw data and detailed results of the analysis can be found at <http://www.fsl.orst.edu/lter/research/intersite/lidet.htm>). We examined how well the data from all sites fit simple mathematical models and the question of whether a 'slow' fraction formed during long-term decomposition by comparing three types of regression models: (1) a simple negative exponential, (2) a negative exponential with an asymptote, and (3) a dual negative exponential model (Wieder & Lang, 1982). Our intent was not to find the single 'best' equation to use or test the best simulation model. Rather, we compared the predictions of these regression models to the observed data and to each other to find cases where a model would apply and if the models predicted similar patterns. Each model is based on different assumptions about the decomposition processes, and because of this, the cases where each model did not apply implies the assumptions were not valid. Both the negative exponential with an asymptote, and dual negative exponential model imply a later, slower decomposition phase, although the asymptotic model implies a rate constant equal to zero is eventually reached.

The first regression model used (Model 1) was a simple negative exponential

$$M_{t1} = M_{01} \times \exp(-k_1 \times t), \quad (2)$$

where M_{t1} is the percent ash-free mass remaining, M_{01} is the initial ash-free mass, t is time in years, and k_1 is the decomposition rate constant in year⁻¹. This model is the one most commonly used to determine the decom-

Table 2 Initial litter substrate quality indices for LIDET study

Species* Leaves*	Samples	Ash (%)	Nonpolar extractives		Water Soluble		Acid Hydrolysable		Acid unhydrolysable†		Tannin		Water soluble carbohydrates		Acid hydrolysable carbohydrates		C (%)	N % ash-free	C/N ratios	AUF/N‡
			% ash-free	% ash-free	% ash-free	% ash-free	% ash-free	% ash-free	% ash-free	% ash-free	% ash-free	% ash-free	% ash-free	% ash-free						
ABCO	3	5.9	17.8	39.4	35.7	7.1	6.0	12.7	9.3	51.3	0.66	78.3	10.9							
ABLA	3	4.3	19.4	32.0	30.6	18.0	6.2	15.9	15.6	54.0	0.71	76.1	25.3							
ACSA	5	4.7	8.2	48.2	27.6	16.0	7.7	11.1	12.7	49.8	0.81	61.8	19.8							
AMBR	5	3.6	6.4	21.7	57.3	14.5	4.7	15.2	36.7	48.6	0.67	73.5	21.7							
ANGE	6	7.7	5.9	14.9	60.3	18.8	1.8	4.0	30.8	44.6	0.62	73.1	30.5							
ANSC	5	3.8	3.9	12.0	71.5	12.7	3.7	6.9	41.1	47.3	0.56	86.1	22.5							
BELU	5	5.7	8.0	18.7	46.3	27.0	2.6	5.7	15.1	49.9	1.60	31.2	16.9							
BOER	5	9.2	5.1	13.4	65.7	15.8	1.2	5.3	34.3	44.9	0.86	52.9	18.3							
BOGR	5	10.2	7.6	14.2	70.12	8.1	1.9	7.5	44.3	43.0	0.96	45.0	8.4							
CEGR	5	4.6	10.8	49.6	27.1	12.5	8.1	17.4	6.7	52.6	1.33	39.7	9.4							
CONU	5	11.7	9.2	52.5	37.6	0.8	9.4	14.5	14.5	47.1	0.81	55.8	1.0							
DRGL	8	7.8	8.0	40.7	13.3	11.0	8.0	13.3	18.1	47.8	1.97	24.2	5.6							
FAGR	5	6.4	7.4	16.3	49.8	26.4	5.3	6.7	21.3	49.4	0.85	58.4	31.0							
GYLU	3	9.0	9.87	40.5	42.9	6.8	5.2	7.4	19.9	43.0	1.37	31.5	5.0							
KOMY	5	5.5	5.4	23.0	62.3	9.3	2.4	8.6	34.8	46.3	1.07	43.9	8.8							
LATR	5	8.0	18.7	32.0	41.1	8.1	5.9	8.6	10.4	50.9	2.14	23.8	3.8							
LITU	5	12.3	14.2	44.8	32.2	8.8	5.2	7.2	16.2	46.4	0.72	65.1	12.2							
MYCE	5	3.8	13.0	29.6	30.4	26.9	6.2	11.4	12.1	52.0	2.11	24.6	12.8							
PIEL	5	1.5	17.4	19.7	41.5	21.5	7.4	6.8	20.3	54.3	0.36	163.8	59.7							
PIRE	5	1.7	15.3	20.7	44.7	19.3	7.4	9.8	20.1	53.4	0.59	92.7	32.8							
PIST	5	3.9	18.9	20.3	40.0	20.8	4.8	7.9	19.6	52.8	0.62	85.9	33.3							
POTR	5	7.7	10.6	28.9	41.4	19.0	4.6	9.8	18.5	49.2	0.74	67.2	25.9							
PSME	9	11.9	13.7	17.2	41.0	28.1	2.9	7.6	24.2	48.8	0.82	59.4	34.2							
QUPR	8	4.4	9.4	27.4	39.6	23.6	6.9	7.1	18.0	51.5	1.03	50.5	23.0							
RHMA	5	4.6	9.0	36.6	37.3	17.1	5.3	17.2	19.6	50.8	0.42	126.3	41.0							
ROPS	6	5.6	34.1	7.2	40.8	17.9	6.3	10.0	11.1	50.2	2.45	20.5	7.3							
SPAL	10	12.2	4.9	27.4	60.46	7.4	4.1	4.7	28.3	42.7	0.71	62.6	10.2							
THPL	7	7.8	14.6	26.3	37.6	21.5	4.4	9.03	16.48	51.1	0.62	83.1	34.5							
TRAE	5	2.8	3.4	6.8	73.6	16.3	2.9	5.0	41.1	47.3	0.38	133.3	43.2							
VOFE	6	5.5	6.7	31.4	42.8	19.1	4.9	9.0	13.0	49.2	1.93	25.6	9.9							
Roots																				
ANGE	8	27.6	6.0	14.0	69.1	10.9	1.1	5.3	33.2	37.0	0.63	59.4	17.3							
DRGL	6	7.0	10.7	20.2	52.8	16.3	2.4	6.7	15.3	48.2	0.76	64.6	21.5							
PIEL	9	6.3	8.9	19.8	36.1	35.2	3.3	8.5	19.7	49.4	0.82	61.5	43.0							
PIRE	3	8.6	6.1	9.4	56.3	28.2	2.3	2.2	13.3	48.4	1.22	39.9	23.2							

Bold-faced species are for the standard litters.

*ABCO, *Abies concolor*, White fir; ABLA, *Abies lasiocarpa*, subalpine fir; ACSA, *Acer saccharum*, sugar maple; AMBR-*Ammohia brevifolulata*, beach grass; ANGE, *Schizachyrium* (aka *Andropogon*) *gerardi*, big blue stem ANSC, *Schizachyrium* (aka *Andropogon*) *scoparium*, little blue stem; BELU, *Betula lutea*, yellow birch; BOER, *Bouteloua eriopoda*, black gramma grass; BOGR, *Bouteloua gracilis*, blue gramma grass; CEGR, *Ceanothus greggii*; CONU-*Cornus nuttallii*, Pacific dogwood; DRGL, *Drypetes glauca*; FAGR, *Fagus grandifolia*, beech; GYLU, *Gymnantheslucida*; KOMY, *Kobresia myosuroides*; LATR, *Larrea tridentata*, creosote bush; LITU, *Liriodendron tulipifera*, yellow poplar; MYCE, *Myrica cerifer*, wax myrtle; PIEL, *Pinus elliotii*, slash pine; PIRE, *Pinus resinosa*, red pine; PIST, *Pinus strobus*, eastern white pine; POTR, *Populus tremuloides*, aspen; PSME, *Pseudotsuga menziesii*, Douglas-fir; QUPR, *Quercus prinus*, chestnut oak; RHMA, *Rhododendron macrophyllum*, Pacific rhododendron; ROPS, *Robinea pseudoacacia*, black locust; SPAL, *Spartina alternifolia*, salt water cordgrass; THPL, *Thuja plicata*, western redcedar; TRAE, *Triticum aestivum*, wheat; VOFE-*Vochlysia ferruginea*.

†This fraction, traditionally called lignin, is more properly termed the acid unhydrolysable fraction (AUF).

‡Traditionally called the lignin:N ratio.

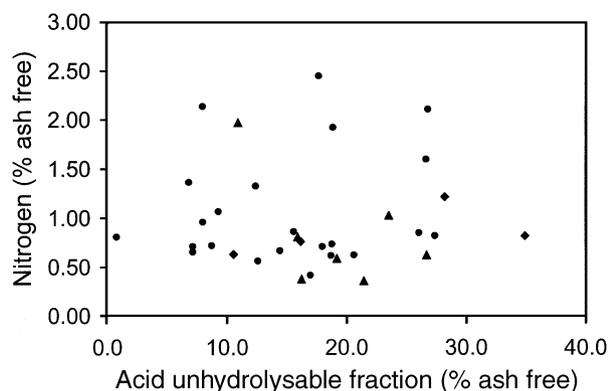


Fig. 3 Range of initial litter nitrogen and acid unhydrolysable fraction (traditionally referred to as lignin) concentrations of the litters used in Long-term Intersite Decomposition Experiment Team (LIDET). Standard leaves indicated by triangles and standard fine roots indicated by diamonds.

position rate (Olson, 1963; Wieder & Lang, 1982; Harmon *et al.*, 1999), particularly for short-term studies.

The second regression model used (Model 2) was also a simple negative exponential, but the solution was constrained so that M_{02} (the y -intercept) ranged between 95% and 105%. Its form was exactly the same as Model 1

$$M_{t2} = M_{02} \times \exp(-k_2 \times t), \quad (3)$$

We used this formulation because Model 1 will estimate an initial mass below 100% if there is an initial rapid drop in mass (Harmon *et al.*, 1990, 1999). Conversely, if there is a lag before the onset of decomposition, Model 1 will estimate an initial mass above 100%. Because we know that the mass started at 100%, Model 2 is constrained by that knowledge.

The third regression model used (Model 3) was a simple negative exponential with an asymptote

$$M_{t3} = M_{03} \times \exp(-k_3 \times t) + S_{03}, \quad (4)$$

where M_{t3} is the percent ash-free mass remaining, M_{03} is the initial ash-free mass of material subject to loss, S_{03} is the asymptote, t is time in years, and k_3 is the decomposition rate constant. This model represents a two-phase decomposition process in which the second phase is completely stable. It implies that there is a fraction of the initial litter that either does not decompose or that new material is formed in the decomposition process that cannot decompose over the time period of observation. Although the model appears to contain three parameters, it has in fact two, because M_{03} and S_{03} sum to 100% and an estimate of one can be used to derive the other.

The fourth regression model used (Model 4) was also a simple negative exponential with an asymptote, but with M_{04} and S_{04} constrained to be within the range of

95–105% of original mass

$$M_{t4} = M_{04} \times \exp(-k_4 \times t) + S_{04}, \quad (5)$$

This model has the same biological meaning as Model 3 and although Model 3 should constrain the initial mass to be 100%, we used Model 4 to assure that this was the case.

The fifth regression model used (Model 5) was a dual negative exponential

$$M_{t5} = M_{f05} \times \exp(-k_{f5} \times t) + M_{s05} \times \exp(-k_{s5} \times t), \quad (6)$$

where M_{t5} is the percent ash-free mass remaining, M_{f05} is the initial ash-free mass of fast material, k_{f5} is the decomposition rate constant of this fast material, M_{s05} is the initial ash-free mass of slow material, k_{s5} is the decomposition rate constant of this slow material, and t is time in years. This model has been used to capture decomposition dynamics in which two different fractions of organic matter are conceived to exist simultaneously, one that decays quickly and the other more slowly, each of which is controlled by its own rate constant. This model has previously been shown to capture the initial rapid loss of material followed by a transition to a slower rate observed in some short-term studies (Blair *et al.*, 1990; Harmon *et al.*, 1990, 1999).

We used nonlinear regression (SAS PROC NLIN with the DUD method) to estimate the parameters of the models (SAS Institute, 1999, SAS Companion for the Microsoft Windows Environment, Version 8, Cary, NC). We avoided removing all except the most obvious outliers from the raw dataset. Means of the percent ash-free mass remaining were calculated for each combination of standard litter and site for a total of 234 cases. Note that although theoretically there could be 243 cases (27 sites \times nine litters), some of the cases were compromised by extreme outliers and/or missing data and were not analyzed. While it was possible to use linear regression models with logarithmic transformation to estimate parameters for Models 1 and 2, this was not possible for the remaining models. We therefore chose to use a uniform method of parameter estimation. In cases where we constrained the initial mass-related parameters, we set bounds for the total initial mass to 95–105% given that variation in replicate samples was approximately 5%. For all the other parameters, we started the 'search grid' of possible parameter values used by the DUD iterative process based on the range of decomposition rate constants observed by earlier analysis of the first 5 years of data (Gholz *et al.*, 2000). If the convergence criteria of the iterative analysis procedure were not met, we readjusted the search grid in terms upper and lower limits and the initial search interval.

This usually resulted in convergence, and in the cases where parameters were estimated using both searches, the parameters were extremely close (i.e. within 1%). We estimated the r^2 of the nonlinear regressions by subtracting the residual sum of squares divided by the corrected total sum of squares from (1). Given the degrees of freedom of our analysis, we determined the number of equations that were significant at the $P < 0.05$ level, which corresponds to an r^2 of 0.85 or greater.

Evaluating the biological realism of models

Once the parameters were estimated, we compared the model predictions to the observed data for each species and site. Rather than use r^2 as the sole index of how well the model fit the observed data, we compared the model predictions to the key biological performance criteria that the initial mass must start at 100% (Fig. 4). Our intent was to determine in how many cases each model matched or was biologically appropriate; one

might think of this as a biologically vs. a statistically determined evaluation. In the case of Model 1, if the initial mass estimated by a regression of mass transformed to natural logarithms was statistically less than <100% based on a one-tailed t -test, then a two-component loss pattern was indicated, and the model was scored as not matching. We also counted the number of cases in which the initial mass was predicted to be <95%, a value based on the typical level of variation expected in the mass remaining. In the case of Model 2, we expected that if a slow fraction exists, this model would tend to over estimate mass in the early stages and underestimate the mass in the later stages of decomposition. This model was scored as not matching if there was a significant and positive time-related trend in the nonlinear regression residuals as indicated by a significant negative y -intercept and a positive slope. In the cases of Models 3 and 4, we also used a regression of the residuals vs. time to test biological realism. The biological realism of the model would be questionable if

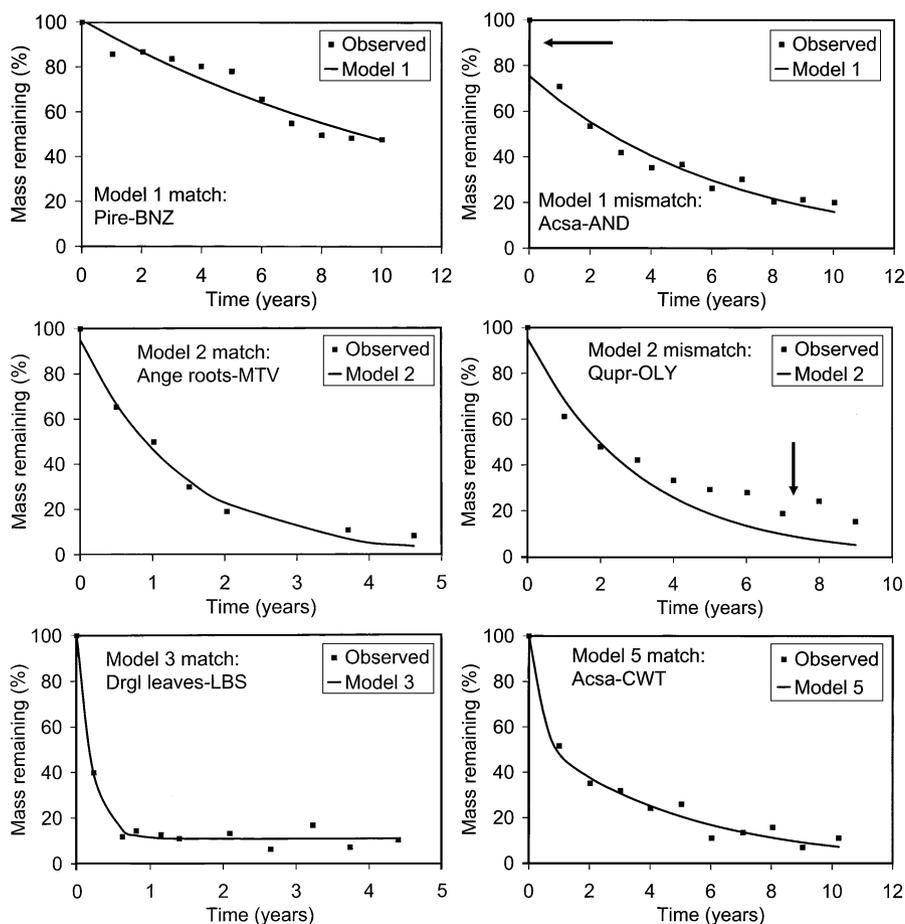


Fig. 4 Examples that matched and mismatched biological performance criteria of models. The criteria differed for the models. For example, for Model 1 we examined the initial mass estimate, but for Model 2 we looked for consistent underestimates in the later stages of decomposition. The arrows indicate the mismatches with observations.

the regression of residuals was significant with a positive y -intercept and a negative slope. This would indicate mass continued to decline, but Models 3 or 4 predicted an asymptote. For Model 5, we considered two possible types of biological mismatches using the regression of the residuals vs. time. If the mass loss data actually indicated an asymptote, then Model 5 should tend to underestimate remaining mass in the later observations. This would be indicated by a negative y -intercept and a positive slope of the residual regression. If the mass loss data followed a simple negative exponential pattern, then Model 5 should overestimate remaining mass in the later observations. This would be indicated by a positive y -intercept and a negative slope to the residual regression.

Estimating long-term integrated decomposition rates

A disadvantage of using models with two components (i.e. Models 3–5) is the difficulty in directly estimating a long-term, average rate of decomposition. This is because the decomposition rate continuously changes over time. We derived a long-term integrated, weighted average decomposition rate by using the predicted mass remaining for Model 5 at time steps of 0.1 years. The sum of these masses over time represents the theoretical accumulation of litter that one would expect given a constant input and the modeled decomposition curve. By then assuming that this represented the steady-state mass (where the input and output fluxes are equal) and that the input was 100 units of mass (i.e. our models were expressed in percent mass remaining), we calculated the time integrated average decomposition rate k_1 using the method of (Olson, 1963)

$$k_1 = 100/M_{ss}, \quad (7)$$

where k_1 is the time integrated average decomposition rate constant, and M_{ss} is the estimated steady-state mass of litter. We used various times of up to 200 years to check if the estimate of k_1 had become time invariant (i.e. an indication the predicted steady-state mass had been reached). We did not use Models 3 or 4 for this estimate because the integral of this function linearly increases once the asymptotic phase is reached; hence there is no steady-state solution.

Evaluating the late, slow phase

In addition to fitting regressions to match the temporal trends in decomposition, we approximated the amount and rate of decomposition of the kinetically defined slow phase. We used two methods to estimate the amount of slowly decomposing material that the models identified. In the first, we used the asymptote

estimated by nonlinear regression. In our second test, we averaged the last four data points for each site/litter combination based on the assumption that this represented the midpoint of material in the later phases of decomposition. This method is likely to overestimate the amount of slow phase material if this phase is not completely reached within the time period covered by the last four data points.

We used two methods to estimate the decomposition rate of the slow phase material. The first was to use the mass specific decay rate (k_{05}) for the slow fraction of Model 5. The second was to use the rate of decomposition estimated by Model 1 (k_{01}) for the last four data points, after removing all the cases in which a simple negative exponential model biologically fit the data because these provided no evidence for a slow fraction.

Results

Final mass remaining

Despite the decade long duration, considerable litter mass remained in some cases after the experiment concluded. The minimum (0.3%) and maximum (79.7%) mass remaining were found at North Inlet and Arctic Lakes, respectively (Table 3). However, there was considerable range within these two sites. For example, Arctic Lakes had a minimum of 32.3%, while North Inlet had a maximum of 58% mass remaining at the last measurement. The degree species differed was indicated in the differences between the maximum and minimum final remaining mass; this ranged between 18% at LaSelva Biological Station and 65% at Jornada.

Evaluating the models

Model 1: the negative exponential. For all litter types and sites, estimates of k_1 for the negative exponential (Model 1) ranged from 0 to 3.471 year⁻¹ and averaged 0.238 year⁻¹. Values of 0 for k_1 did not indicate that there was no decomposition at all; in this particular case, M_{01} was 57% of initial mass, indicating a rapid initial loss followed by minimal decomposition. This reveals a shortcoming in Model 1 for representing such a wide range of litter \times site combinations. Nonlinear regressions using this model produced r^2 -values that ranged from <0.01 to 0.99, with a mean of 0.78. The model developed from nonlinear regression predicted over 85% of the variation in 48% of the cases (indicating they were significant), and therefore this model appears to be able to predict decomposition dynamics of many cases adequately. For the natural logarithm transformed regression, the single exponential model was significant ($P < 0.05$) for 87% of the cases, indicating that our

Table 3 The mean final percent mass remaining at the end of the experiment for sites and species

Site code	Species and litter type								
	<i>Acer saccharum</i>	<i>Andropogon gerardi</i>	<i>Drypetes glauca</i>	<i>Drypetes glauca</i>	<i>Quercus prinus</i>	<i>Thuja plicata</i>	<i>Triticum aestivum</i>	<i>Pinus</i> spp.*	<i>Pinus</i> spp.*
	Leaf	Root	Leaf	Root	Leaf	Root	Leaf	Leaf	Root
AND	19.98	19.04	5.89	15.60	20.28	25.99	20.59	21.92	44.13
ARC	32.33	50.03	36.47	64.82	36.11	45.89	46.00	63.83	79.71
BCI	6.92	12.58	2.88	17.52	9.09	15.83	8.38	46.35	55.66
BNZ	30.87	35.92	32.62	44.91	34.23	45.24	27.09	47.71	65.09
BSF	50.32	40.18	24.00	49.27	49.00	50.87	34.00	64.77	55.64
CDR	35.38	14.60	13.28	4.78	29.02	21.87	3.77	23.48	31.79
CPR	41.29	21.00	27.17	25.04	31.09	73.45	34.97	44.26	66.00
CWT	11.04	11.60	2.64	11.81	4.86	20.42	7.98	9.47	42.60
GSF	52.16	18.33	35.40	10.71	41.17	57.11	15.18	64.87	45.63
HBR	23.14	10.88	9.49	21.77	14.94	23.48	8.78	13.04	44.54
HFR	10.42	16.42	11.14	19.83	12.03	18.57	13.19	26.00	47.59
JRN	0.11	25.07	30.06	28.22	37.05	27.72	6.33	7.69	65.03
JUN	30.59	27.44	18.14	46.26	28.17	43.41	30.79	40.46	60.56
KBS	7.29	5.51	5.19	37.41	9.03	30.61	2.64	44.63	25.91
KNZ	31.57	10.13	5.37	21.96	54.36	47.14	19.04	26.85	33.18
LBS	13.20	5.15	9.97	11.58	18.35	15.36	16.20	19.26	23.47
LUQ	15.97	9.39	7.16	17.93	12.11	22.10	9.58	28.34	40.28
LVW	52.10	36.69	31.04	37.29	49.23	53.12	29.47	64.51	63.06
MTV	16.25	8.10	9.24	8.06	17.20	27.21	10.65	35.60	18.31
NIN	9.44	53.66	0.59	58.32	4.49	10.87	0.03	8.20	52.11
NLK	50.99	55.66	45.69	63.96	68.45	68.49	65.46	75.22	78.47
NWT	36.06	46.89	37.59	39.44	47.89	69.88	43.90	56.39	70.52
OLY	19.48	18.32	8.29	22.99	15.22	16.11	6.36	27.01	37.57
SEV	35.74	33.52	58.76	36.00	64.61	66.17	50.89	52.36	70.23
SMR	63.60	9.42	30.83	15.76	49.25	50.87	32.51	48.53	32.41
UFL	16.55	3.29	2.76	8.36	8.89	21.50	6.28	28.24	34.81
VCR	20.63	50.25	4.67	50.09	8.63	41.19	0.07	47.08	62.26

*The species of *Pinus* used varied by site and root vs. leaf.

nonlinear significance test was conservative. A comparison to the observations with respect to our 'biological criteria' indicated that Model 1 had an initial mass <95% for 73% of the total cases examined ($N = 234$), indicating the possibility of a biologically unrealistic model. A one-tailed t -test indicated that in 35% of the cases the y -intercept was significantly ($P < 0.05$) lower than 100%; given our degrees of freedom for the regressions, this is likely to be a conservative estimate.

The degree to which cases matched our criterion for Model 1 depended on the litter species and type incubated. Analyzed at the level of species and type of litter only *Pinus resinosa* roots did not have an initial mass that was significantly lower than 100%. To illustrate how well the models matched the data we graphed two contrasting litter types: *Pinus* and *Drypetes* leaves; see Fig. 5. For *P. resinosa* leaves, the major mismatch between predictions and observations was

that the initial mass was predicted to be <100%, although there were also cases in which a lag was evident. For *Drypetes* leaves, the simple negative exponential best fit the middle stages of decomposition and generally underestimated the initial mass as well as overestimated losses in the later stages of decomposition. Analysis at the level of sites indicated that for 13 of the 27 sites, the initial mass was not significantly different than 100%; these were typically drier sites (Central Plain-Short Grass Steppe, Jornada, and Sevilleta) or those with a dry season at the start of the experiment (Barro Colorado Island).

Model 2: constrained negative exponential. For all litter types and sites, estimates of k_2 for the negative exponential constrained to have an initial mass of 100% (Model 2) ranged from 0 to 3.159 year^{-1} and averaged 0.400 year^{-1} . The k_2 of 0 year^{-1} was for *Pinus elliottii* roots at Niwot Ridge, a site that generally had

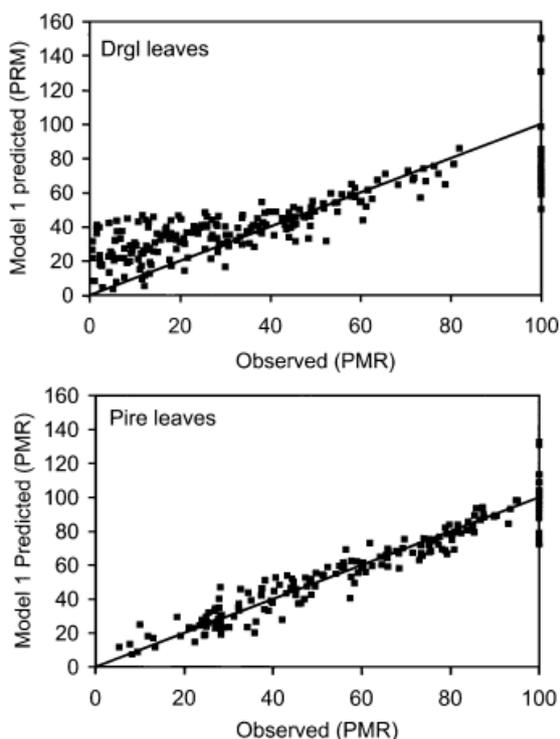


Fig. 5 Remaining mass predicted by the simple negative exponential regression (Model 1) vs. the observed data for two representative litter types. PMR is percent mass remaining; the 1:1 line is shown.

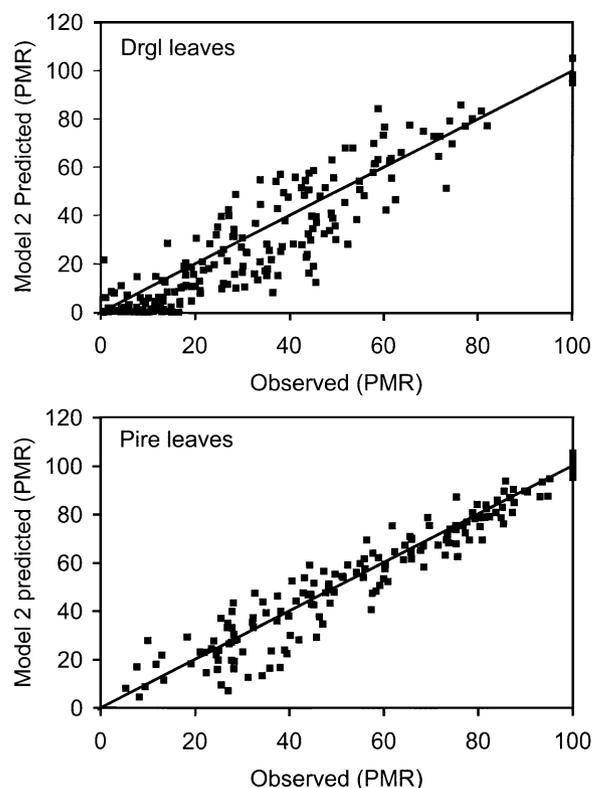


Fig. 6 Remaining mass predicted by the simple negative exponential regression with initial mass constrained to 100% (Model 2) vs. the observed data for two representative litter types. PMR is percent mass remaining; the 1:1 line is shown.

$k_2 > 0.10 \text{ year}^{-1}$. Nonlinear regressions using this model produced r^2 -values that ranged from <0.01 to 0.99, with 0.67 as the mean.

This model predicted over 85% of the variation in 30% of the cases, a lower proportion than for the simple negative exponential model. However, we selected this model because of its diagnostic potential; it should deviate from the observations in a predictable manner by underestimating mass in later stage of decomposition if there was a slow phase of decomposition. An analysis of the residuals from the nonlinear regressions indicated that in 52.4% of the cases that there was a significant relationship between the residual and time, with 43.6% having a negative y -intercept and a positive slope. This would indicate Model 2 tended to underpredict mass in the later stages of decomposition for many cases.

As with Model 1, the degree to which this model biologically matched depended on the species, with *P. resinosa* roots being the only litter type that did not have a significant residual regression. In the case of *P. resinosa* leaves, adding the constraint to the negative exponential removed the mismatch between predictions and observations for initial mass (Fig. 6). For *Drypetes* leaves, Model 2 generally underestimated

the mass in the later stages of decomposition, but the initial mass constraint imposed allowed this model to match the earlier stages of decomposition better. Also as with Model 1, there was a pattern of variation in the adequacy of Model 2 among sites, with drier sites more likely to conform to Model 2 than wetter sites.

Models 3 and 4: negative exponential model with an asymptote. For all litter types and sites, estimates of k_3 for the negative exponential with an asymptote (Model 3) ranged from 0.072 to 4.98 year^{-1} and averaged 0.721 year^{-1} . Nonlinear regressions using this model produced r^2 -values that ranged from <0.01 to 0.99 with a mean of 0.77. This model was statistically significant and predicted over 85% of the variation in 46% of the cases, thus predicting decomposition dynamics about as well as Model 1. A striking result was that regression of residuals was significant in 11.9% of the cases examined and that a positive y -intercept and negative slope occurred in only 4% of the cases. This would indicate this model matched our biological criteria for $\sim 95\%$ of the total cases examined ($N = 234$).

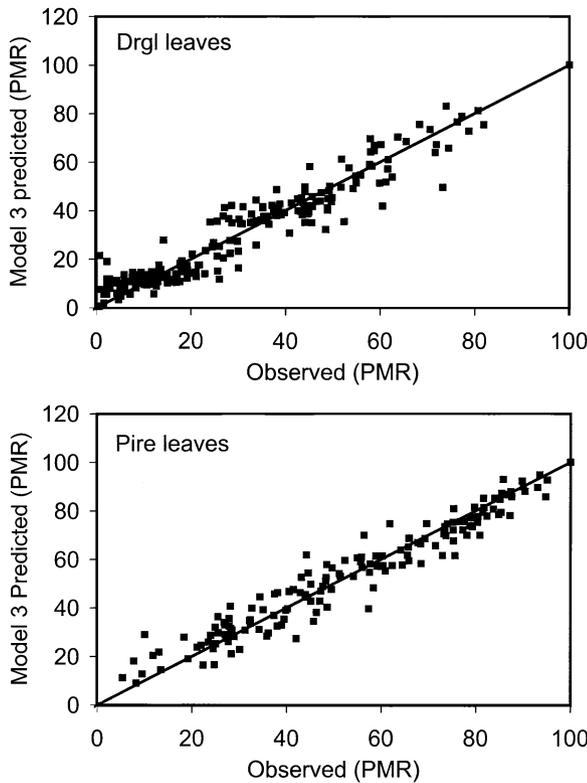


Fig. 7 Remaining mass predicted by the negative exponential and asymptotic regression (Model 3) vs. the observed data for two representative litter types. PMR is percent mass remaining; the 1:1 line is shown.

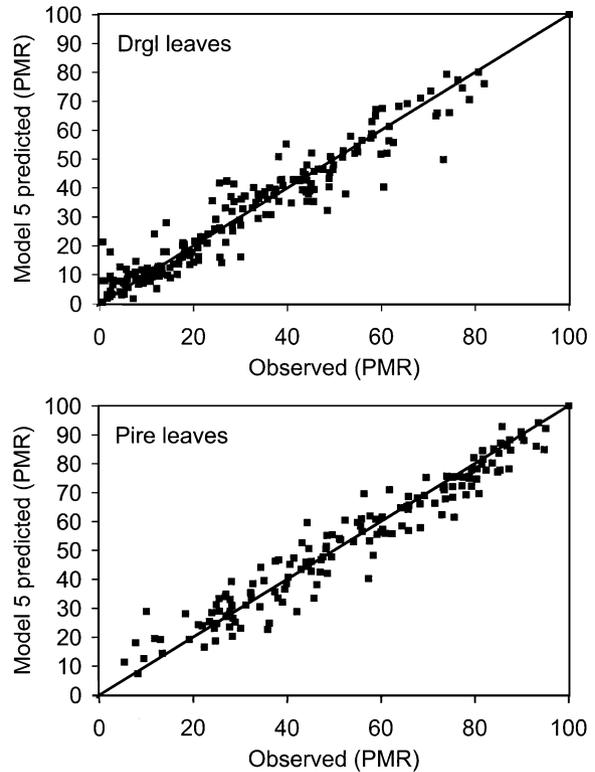


Fig. 9 Remaining mass predicted by the dual negative exponential regression (Model 5) vs. the observed data for two representative litter types. PMR is percent mass remaining; the 1:1 line is shown.

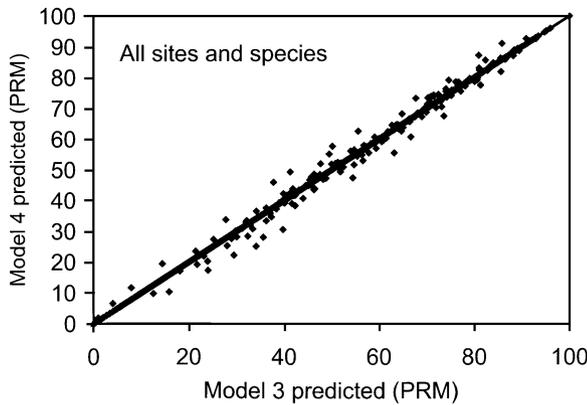


Fig. 8 Relationship between predictions of Models 3 and 4. Both models are negative exponential and asymptotic regressions, but Model 4 has the initial mass constrained to 100%. PMR is percent mass remaining; the 1:1 line is shown.

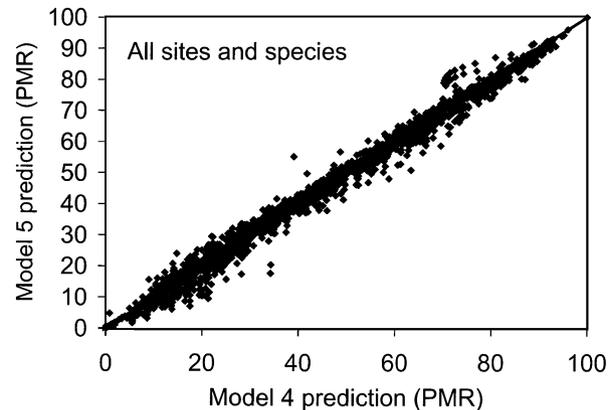


Fig. 10 Relationship between predictions of Model 4 (with asymptote) and Model 5 (dual exponential) for all species and sites. PMR is percent mass remaining; the 1:1 line is shown.

In the case of both *P. resinosa* and *Drypetes* leaves, the major mismatch between predictions and observations was that there was a tendency for mass in the later phases of decomposition at first to be underestimated and then to be overestimated as decomposition progressed (Fig. 7). This pattern would be expected if

some decomposition occurred during the slow phase, because the asymptote represents an average of these two time periods.

The results for Model 4 were very similar to those of Model 3 and therefore a detailed description of that analysis is omitted (Fig. 8).

Model 5: the dual exponential regression model. The dual exponential regression (Model 5) produced r^2 -values that ranged from 0.14 to 0.999 with a mean of 0.77 for all litter types and sites. This model was statistically significant and predicted over 85% of the variation in 59% of the cases. Based on purely statistical criterion this model predicts decomposition dynamics best across the range of litter types and sites we analyzed. Consistent with this finding, the regression of residuals against time indicated significant regressions in 10.2% of the cases. For 0.4% of the cases, a negative y -intercept and positive slope was found, indicating an underestimation of mass remaining in the later stages of decomposition. This would indicate an asymptotic phase. For 2% of the cases, the regression had a significant positive y -intercept and a negative slope, indicating the mass remaining was overestimated as would be expected if the mass loss pattern was a negative exponential. This would indicate that Model

5 matched biological criteria for $\sim 97\%$ of the 234 cases examined.

For both *P. resinosa* and *Drypetes* leaves, the major mismatch between predictions and observations was that there was a tendency for mass in the later phases of decomposition to be overestimated by the model (Fig. 9). We expected this to occur if decomposition in the later phases was faster than indicated by k_{s5} (i.e. the rate constant controlling the slow fraction) during this period. Despite slight differences, the predictions of Models 4 and 5 were very similar (Fig. 10). Based on r^2 -values and the degree they biologically match with the cases examined, it would be difficult to objectively select between the two models. In other words, we found that overall patterns of decay over the 10-year period could be characterized equally well if late-stage decay were represented by an asymptote or by a second component, with a lower rate constant.

Estimates of long-term integrated decomposition rate

The estimates of the long-term average or integrated decomposition rate (k_i) ranged from 0.017 to 4.653 year⁻¹ and averaged 0.353 year⁻¹. These values are considerably lower than the first-year decomposition rate constant, which ranged from 0.034 to 4.766 year⁻¹ and averaged 0.51 year⁻¹. Thus while not all cases exhibited a slow phase of decomposition, it was prominent enough that, on average long-term integrated decomposition rate constant was roughly 70% of the short-term decomposition rate constant.

A regression of the integrated k against the 1-year k across all 234 cases indicated that the former was 75% of the latter on average (Fig. 11a); however, in 18% of the cases the integrated k was higher than the 1-year k indicating a possible lag in decomposition (Fig. 11b). The ratio of the integrated k to the 1-year k was most likely to exceed 1 when the 1-year k dropped below 0.5 year⁻¹. For the majority of cases it appears that 1-year estimates are higher than long-term decomposition rate constants, indicating that models using short-term rates will underestimate litter stores.

Evaluating the slow phase: decomposition rate and amount of material

The range in slow decomposition rate constants, as indicated by the mass loss during the last four time points for the species that did not conform to the simple negative exponential model was 0–1.34 year⁻¹, with a mean of 0.221 year⁻¹. This wide range is largely related to differences in site conditions. For example, the range at the coldest site, Arctic, was 0.014–0.104 year⁻¹,

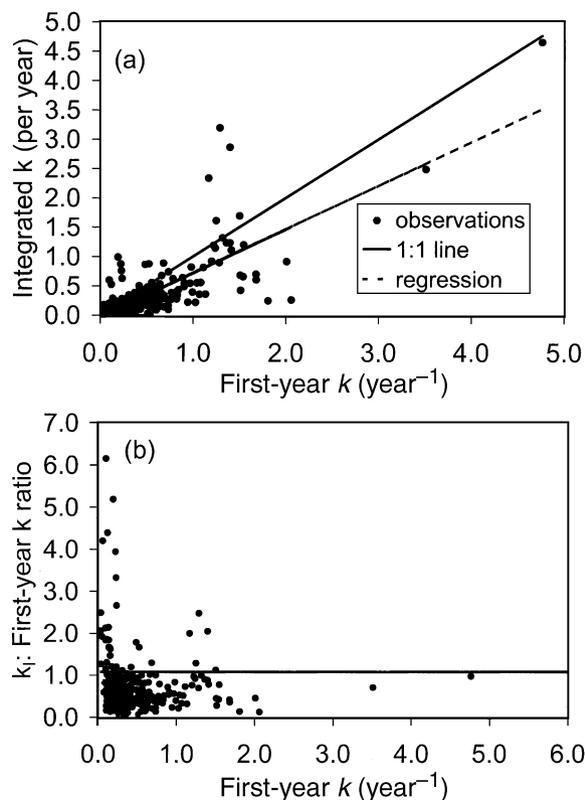


Fig. 11 Relationship of the integrated, weighted average decomposition rate vs. that estimated from 1 year of decomposition. (a) Comparison of the integrated vs. the 1-year decomposition rate. The regression equation is $Y = -0.03 + 0.75 \times X$, $r^2 = 0.59$. (b) Ratio of the integrated k and the 1-year k vs. the 1-year decomposition rate. The horizontal line indicates a ratio of 1, the expected case when there was no slow phase of decomposition.

whereas the range at one of the warmest sites (LaSelva) was 0.23–0.80 year⁻¹. There were also differences among species, but the range of averages among species was smaller than sites: 0.059 year⁻¹ for *P. elliotii* fine roots to 0.47 year⁻¹ for *Triticum aestivum* as compared with a site range of 0.057–1.073 year⁻¹ (at Arctic and Luquillo, respectively).

Across all sites and litter types the range of slow fraction decomposition rates [k_{s5} in Eqn (6)] estimated from Model 5 indicated that the decomposition rate constant of the slow material ranged from 0 to 1.46 year⁻¹ and averaged 0.139 year⁻¹. These rates were lower than that estimated for the last four data points, which is consistent with our finding that, in inspecting the curve fits of Model 5 for biological realism, we noted that Model 5 tended to overestimate mass remaining in the latest stage of decomposition. The slow fraction decay-constants from Model 5 were also considerably lower than the estimates of decomposition rate constants for the 'fast' fraction, which ranged from 0.06 to 76 year⁻¹ and averaged 9.73 year⁻¹. This result indicates that in many cases the fast phase of decomposition was completed within a year. The species averages of the decomposition rate of the slow fraction of litter (k_{s5}) ranged from 0.06 year⁻¹ for *P. elliotii* fine roots to 0.178 year⁻¹ for *Quercus prinus* leaves. The site averages of k_{s5} ranged from 0.042 year⁻¹ for Loch Vale to 0.687 year⁻¹ for Luquillo.

Although the values of k_{f5} and k_{s5} [Eqn (6)] provide no direct information about the amount of slow-decaying substrate, our method of fitting regressions did fit the constants M_{f05} and M_{s05} [Eqn (6)] representing the portions of initial mass subject to decomposition at each of the two rate constants. The amount of slow material (M_{s05}) appeared to be a function of both site characteristics and substrate quality. Similarly, Models 3 and 4 provided estimates of slow fraction masses S_{03} [Eqn (4)] and S_{04} [Eqn (5)], respectively. Based on these estimates of asymptotic mass, the slow fraction was equivalent to 0–73% of the initial mass across our range in litter types and sites. Those regression estimates with little to no slow fraction material were cases where a simple negative exponential model closely matched the temporal pattern (e.g. *P. resinosa* leaves). The average of the asymptotic mass was 32% of the initial mass, with the species average ranging from a low of 15% for *T. aestivum* to a high of 45% for *P. elliotii* fine roots. The range among site averages was even wider, ranging from 3.8% at Luquillo to 51% at Loch Vale. In general, as the climatic favorability for decomposition of a site increased, the amount of slow material decreased. Similar patterns were revealed by the average of the last four observations of mass remaining, which ranged among all the cases from 2.8% to 80% of ash-free mass.

The range in averages for species was from 17% for *Drypetes* leaves to 52% for *P. elliotii* fine roots. The range among site averages was somewhat wider with 13% at LaSelva and up to 56% at Loch Vale.

Discussion

Evaluating models of decomposition

We selected a range of regression models that had meaningful biological interpretations and that have been applied in the past. Our primary purpose of using these models was not to find the 'best' model, as that is likely to depend on the type of litter, the environment, and the length of time of the measurements. For some species and substrates (e.g. *Pinus* leaves) a simple negative exponential model appears to match biological criteria particularly well. For others (e.g. *Drypetes* leaves), a simple negative exponential model does not often match the reasonable biological expectation that the initial mass start at 100%. For short-term studies that end before the slow fraction becomes evident, a single negative exponential model will most likely fit observations (although not if there are large initial rapid losses of very labile fractions).

It is tempting to use the single negative exponential model as it has the most convenient equation for simple parameterization. However, our analysis shows that a more complex model (Model 5) provides the most generally acceptable set of curve fits to data across a wide range of litters and sites. Moreover, Model 5, the dual exponential, is the most general case and simplifies to the other models. When a slow fraction is not present, it simplifies to Models 1 or 2. Alternatively, when the slow fraction has an undetectable rate of decomposition, it simplifies to Models 3 or 4 which includes an asymptote representing a stable fraction. On this basis, we recommend that a dual exponential model is the logical starting place for any analysis of long-term decomposition patterns. Models 3, 4, and 5 appear to fit the data equally well in terms of statistical measures of fit such as r^2 , P -values, or mean square error. Information not present in the LIDET dataset, such as direct measures of the rate of decomposition of the slow fraction would be needed to distinguish among them.

Other models, particularly simulation models, might be even better than those considered here. Given our sample size for each litter type and site combination, we could not use linear regression methods to estimate parameters for a three-component model. However, using a simulation modeling framework, this is possible and there are indications that this improves the match with observed data (Coûteaux *et al.*, 1998; Adair *et al.*, 2008). Biologically this probably does provide increased

realism because it could capture a rapid loss of labile material, an intermediate stage dominated by structural compounds but still undergoing significant decomposition (Coûteaux *et al.*, 1995), and a slow phase or limit value (Aber *et al.*, 1990; Berg, 2000a,b). It may also be advantageous to consider a continuous range of substrate quality (Ågren & Bosatta, 1987) or the generation of slower decomposing secondary material by decomposers in more mechanistic models.

Estimating long-term decomposition rates

The observation that in many cases a simple negative exponential model cannot be used has implications for how species are compared and how decomposition data are used. With a simple negative exponential model the relative ranking of species is time invariant. However, with either an asymptote or a dual exponential model it is possible that the relative ranking is a function of time, making one-time comparisons of species problematic. Our integrated, weighted average rate constant (k_i) provides a time invariant ranking of species and sites. This integrated rate is also most useful for aggregated ecosystem models that consider a single overall pool of litter vs. models that track cohorts of litter (Pastor & Post, 1986), or ones that track fast and slow fractions separately (Parton *et al.*, 1987, 1994; Currie & Aber, 1997).

In 18% of the cases the integrated k was higher than the 1-year k : six sites (Central Plains-Shortgrass Steppe, Jornada, Juneau, North Temperate Lakes, Santa Margarita, and Sevilleta) accounted for the majority (i.e. 82%) of these cases. With the exception of Juneau and North Temperate Lakes, these were dry sites in which colonization by decomposers might have been slow or dependent on the arrival of a wet year. Alternatively, these are sites where photodegradation is highly likely and slow initial biological decomposition might be followed by more rapid physical degradation (Parton *et al.*, 2007). In the case of North Temperate Lakes, the shorter timeframe of the experiments at that site have might have precluded the development of a slower phase of decomposition. For Juneau, the incorporation of the litterbags into the deep moss layers at that site might have caused decomposition rates to increase over time by increasing litter moisture content.

In addition to being slower than short-term decomposition rate constants, it is possible that long-term decomposition processes are under a different set of controls than those of initial decomposition. W.S. Currie *et al.* (unpublished data) examined the degree climate and substrate quality indices correlated with long-term decomposition rate constants. While climatic indices, such as CDI and AET, and substrate quality indices,

such as, lignin, N, acid-hydrolysable fraction, and tannin content, were correlated to k_i , these correlations were much weaker than for short-term decomposition rate constants. This implies that as decomposition advances, differences in litter types and places tend to decrease.

Evaluating the presence of a slow phase

The inter-relationship of the mathematical models we analyzed yields insight into when and where there is a slow fraction. It must be borne in mind that the slow phase is operationally defined. One cannot actually measure it directly because chemically it represents a poorly understood, complex mixture of materials (Swift *et al.*, 1979; Melillo *et al.*, 1989; Kögel-Knabner, 2002). If we define the slow phase as causing a deviation from the simple negative exponential model, then we can conclude that in many cases, some slow material influenced the temporal trend in mass remaining. However, there are also many cases in which a slow fraction need not be invoked to explain the temporal pattern of mass loss. While it would be ideal if deviations from the single exponential model could be predicted from substrate quality or site conditions, we did not find any obvious relationships that could be used in a predictive model. As suggested in W.S. Currie *et al.* (unpublished data) there may be interactions between the litter in the bags and the surrounding litter that may influence the pattern and rate of decomposition.

We observed a wide range in the amount of slow material that is estimated across the LIDET experiment. It appears to be lower at sites with environments more conducive to rapid decomposition, but the differences among species remain relatively constant. This may indicate that the rate at which slow material is decomposed is a function of the site environment, while the amount of slow-material precursor compounds initially present is a property of the species of litter. W.S. Currie *et al.* (unpublished data) found that climate indices, such as CDI and AET, and substrate quality indices, such as lignin, acid-hydrolysable fraction, and tannin, were correlated to the size of the slow pool. However, the coefficients of determination for these regressions was <21%, supporting the lack of clear trends found in our preliminary analysis.

Although the latter stages of decomposition have been referred to as a stable phase (Melillo *et al.*, 1989; Aber *et al.*, 1990), decomposition appears to be detectable over the time-span of a decade. Our analysis indicates a decomposition rate of the slow fraction of $>0.01 \text{ year}^{-1}$, with most of the estimates being an order of magnitude higher. This is in contrast to the decomposition rates of mineral soil organic matter, which

tends to have decomposition rate constants of $<0.01 \text{ year}^{-1}$ (Gaudinski *et al.*, 2000; Trumbore, 2000). Therefore, one might conceive of the slow litter material as being the precursor to soil organic matter that is complexed with mineral material, with the slow component of litter having a faster rate of mass loss than soil organic matter.

Our estimates of decomposition rates of the slowly decomposing material are relatively crude. A more controlled study, starting with a known quantity of this material and examining its dynamics using stable isotope enrichment would greatly improve understanding of the factors controlling the degradation of this complex material. Better chemical and kinetic characterization of the nature of the slow material might also provide insights into how this material is formed during decomposition. If on one hand, the slow material is simply a residual recalcitrant fraction initially present in the litter (e.g. as proposed by Coûteaux *et al.*, 1995), one would predict that the input is controlled by the type of litter and its rate of decomposition controlled by the site physical environment and biota. If on the other hand, this material is formed by decomposers from the original material (as proposed by Kögel-Knabner, 2002), then both the input and decomposition of this material are likely to be controlled by the site physical environment and biota.

There is an important global-scale implication of the presence or absence of a later, slowly decomposing fraction in plant litter. Global estimates of litter stores have rarely been directly estimated as in the case of mineral soil carbon (Post *et al.*, 1982; Jobbagy & Jackson, 2000), although the work of Matthews (1997) is an exception. Estimates of pool sizes are typically derived from litterfall rates combined with estimates of decomposition rate constants. Our study indicates that short- and long-term decomposition rates are not similar, and in the majority of cases (82%) the average, long-term decomposition-rate constant is lower than the 1-year decomposition rate constant. A rough global impact on the difference in estimates of litter stores can be derived by dividing the input flux by the decomposition rate constant (Olson, 1963). This indicates that if 1-year decomposition rate constants are used in these estimates, litter pool sizes are likely to be underestimated by at least 34% relative to those using long-term rate constants. Our analysis indicates that the negative exponential model is appropriate for the many species and site combinations examined (27–65% depending on the test used). Further, our estimates of an integrated decomposition rate constant, representing a weighted average, are on average 75% that of 1-year decomposition rate constants, an observation consistent with the presence of a slower phase of decomposition. While our study has focused on the biological degradation of litter,

there are many systems where fire removes a large fraction of organic material added to the system. Sites and litter types that exhibited an asymptotic pattern of litter decomposition, may accumulate considerably less litter than our equations indicate if fires are frequent. A more detailed analysis of the degree to which litter stores have been underestimated and relative balance of biotic vs. abiotic (i.e. fire) losses is therefore warranted.

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