Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition

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Abstract

We analysed data on mass loss after five years of decomposition in the field from both fine root and leaf litters from two highly contrasting trees, *Drypetes glauca*, a tropical hardwood tree from Puerto Rico, and pine species from North America as part of the Long-Term Intersite Decomposition Experiment (LIDET). LIDET is a reciprocal litter-bag study involving the transplanting of litter from 27 species across 28 sites in North and Central America reflecting a wide variety of natural and managed ecosystems and climates, from Arctic tundra to tropical rainforest. After 5 years, estimated *k*-values ranged from 0.032 to 3.734, lengths of Phase I (to 20% mass remaining) from 0.49 to 47.92 years, and fractional mass remaining from 0 to 0.81. Pine litter decomposed more slowly than *Drypetes* litter, supporting the notion of strong control of substrate quality over decomposition rates. Climate exerted strong and consistent effects on decomposition. Neither mean annual temperature or precipitation alone explained the global pattern of decomposition; variables including both moisture availability and temperature (i.e. actual evapotranspiration and DEFAC from the CENTURY model) were generally more robust than single variables. Across the LIDET range, decomposition of fine roots exhibited a Q_{10} of 2 and was more predictable than that of leaves, which had a higher Q_{10} and greater variability. Roots generally decomposed more slowly than leaves, regardless of genus, but the ratio of above- to belowground decomposition rates differed sharply across ecosystem types. Finally, *Drypetes* litter decomposed much more rapidly than pine litter in 'broadleaved habitats' than in 'conifer habitats', evidence for a 'home-field advantage' for this litter. These results collectively suggest that relatively simple models can predict decomposition based on litter quality and regional climate, but that ecosystem-specific problems may add complications.

Keywords: climate, decomposition, *Drypetes glauca*, LIDET, model, pine

Introduction

Concerns over climatic change have spurred the development of ecosystem models with sufficient generality to run at global scales. Such models now play a key role in predicting not only the response of ecosystems to climate change, but also their feedback effects on climate. In particular, the fluxes and pools of carbon (C) in terrestrial

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ecosystems are major components of the global C budget. Numerous studies have addressed the effects of increased atmospheric CO_2 concentrations and/or altered climate on the physiological responses of plants and ecosystem primary production (e.g. Melillo *et al.* 1993). The largest pool of C in terrestrial ecosystems, however, is not living organic matter ($\approx$ 550 TgC), but plant detritus and soil organic matter (*c.* 1200 TgC; Moore & Braswell 1994). Schlesinger (1991) estimates that global terrestrial hetero-

trophic respiration equals ≈ 60 Tg Cy^{-1}, 11 times the annual amount of CO_2 released by fossil fuel consumption and industrial activity. This heterotrophic respiration results from the decomposition of above- and below-ground plant detritus, and to a lesser degree, that of older soil organic matter. Thus, global ecosystem C models and budgets must incorporate the factors governing decomposition over a broad range of ecosystems, plant functional groups and climates. These models must also predict how decomposition rates and detrital C pools will change with increased temperature, altered rainfall, increased atmospheric CO_2 and other components of global change. However, for the most part, existing models (e.g. Agren *et al.* 1991; Running & Gower 1991; Melillo *et al.* 1993) rely on a few proposed direct relationships between climate and litter quality. Although such relationships have been supported empirically for certain types of litter, in particular ecosystems, usually with 1–2 years of data, and over some range in climate, they have not been tested globally (either in terms of litter quality or climate) or using long-term data.

At the global scale, it is clear that climate affects decomposition (Olson 1963). It is also clear that both the C chemistry and nutrient (especially N) concentrations of litter, or the ratios of C fractions to nutrient concentrations, strongly affect decomposition (Aber *et al.* 1990). A few studies have compared different litter types across climatic gradients or ecosystem types. Based on these studies, decomposition models incorporating various litter quality and climate parameters have been proposed (e.g. Meentemeyer 1978; Aerts 1997).

The Long-Term Intersite Decomposition Experiment (LIDET) was initiated in 1989 to study the effects of substrate quality and global macroclimate on decomposition and nutrient release from fine litter over a 10-y period (LIDET 1995). The overall project is a reciprocal litterbag study involving the transplanting of leaf and root litter from 27 species across 28 sites in North and Central America reflecting a wide variety of natural ecosystems and climates, from Arctic tundra to tropical rainforest (Table 1).

LIDET significantly expands the experimental basis upon which to develop models. For example, Aerts (1997) used a synthesis of published data to derive a model, similar to the earlier model of Meentemeyer (1978), covering a range of climate conditions comparable to that of LIDET, but only for the first year of decomposition and only for leaves decomposing above ground. Aert's analysis, as Meentemeyer's, did include a broader range of leaf litter qualities than in LIDET. Long-term studies of decomposition have taken place (e.g. the five-year study of Berg and colleagues in Sweden; Berg *et al.* 1982; Berg & Ågren 1984), but usually with single substrates and/or a limited environmental range. The vast majority of litter decomposition studies and models have used above-ground litter only, yet much of NPP occurs and is decomposed below ground (Vogt *et al.* 1986), indicating another significant data gap.

In this paper, we analyse data on mass loss after five years of decomposition in the field from both fine root and leaf litters from all the LIDET sites, and from two highly contrasting trees: *Drypetes glauca*, a tropical hardwood tree from Puerto Rico, and pine species from North America (fine roots from *Pinus elliottii and* leaves from *Pinus resinosa*). *Drypetes* and *Pinus* were the only genera for which both leaves and fine roots were included at all the LIDET sites over the entire five years.

Hypotheses tested

We tested four hypotheses utilizing this LIDET data subset.

Hypothesis 1—Climate effects on decomposition. Temperature and moisture regulate decomposition, but simple climate indices will be less predictive than more complex ones that express interactions of temperature and moisture. Actual evapotranspiration (AET), one such synthetic climate variable, is widely correlated with primary production on regional and global scales (Rosenzweig 1968; Webb *et al.* 1978) and has previously been used as a climate variable in models predicting regional or global rates of decomposition (Meentemeyer 1978, 1984). In this study, we also consider DEFAC, another synthetic climate variable used to predict decomposition rates in the ecosystem model, CENTURY (Parton *et al.* 1989, 1994), that treats the interaction of temperature and moisture differently.

Hypothesis 2—Substrate quality effects on decomposition. The relative differences in decomposition rates between high- and low-quality litters are similar across ecosystem type and climate. An alternative hypothesis is that the relative behaviour of low- and high-quality litters differs in certain ecosystems or for some climates. In this study, we consider litter quality as a qualitative variable by contrasting the decomposition of litter from two widely dissimilar species, *Drypetes* and pine. In other words, we used litter quality as a categorical variable in models examining the interactions of quality with continuous climate variables. Because the LIDET study also examined 23 other litter types not discussed here, other papers will consider the quantitative effects of various litter quality parameters (e.g. percentage lignin or N) on decomposition.

Hypothesis 3—Above- vs. belowground decomposition. The climatic responses of leaf litter and root litter decom-

Table 1 The LIDET sites, names, locations, team members representing sites and latitudes and longitudes of the sites (alphabetical by site acronym)

Site (acronym)	Location	Team member	Latitude – longitude
H.J. Andrews Exper. Forest (AND)	Oregon	Mark Harmon	44°14′ N – 122°11 W
Arctic Tundra (ARC)	Alaska	Jim Laundre	63°38′ N – 149°34′ W
Barro Colorado Island (BCI)	Panama	Joseph Wright	9°10′ N – 79°51′ W
Bonanza Creek Exper. Forest (BNZ)	Alaska	Keith Van Cleve	64°45′ N – 148°00′ W
Blodgett Research Forest (BSF)	California	Steve Hart	38°52′ N – 105°38 W
Cedar Creek Natural History Area (CDR)	Minnesota	Dave Wedin	45°24′ N – 93°12′ W
Central Plains Exper. Range (CPR)	Colorado	Indy Burke	40°49′ N – 104°46′W
Coweeta Hydrological Laboratory (CWT)	North Carolina	Barry Clinton	35°00′ N – 83°30′ W
Guanica State Forest (GSF)	Puerto Rico	Ariel E. Lugo	17°57′ N – 65°52′ W
Hubbard Brook Exper. Forest (HBR)	New Hampshire	Tim Fahey	43°56′ N – 71°45′ W
Harvard Forest (HFR)	Massachussets	Jerry Melillo	42°40′ N – 72°15′ W
Jornada Exper. Range (JRN)	New Mexico	Walter Whitford	32°30′ N – 106°45′ W
Juneau (JUN)	Alaska	Paul Alaback	58°00′ N – 134°00′ W
Kellogg Biological Station (KBS)	Michigan	Eldor Paul	42°24′ N – 85°24′ W
Konza Prairie Research Natural Area (KNZ)	Kansas	Tim Seastedt	39°05′ N – 96°35′ W
La Selva Biological Station (LBS)	Costa Rica	Phil Sollins	10°00′ N – 83°00′ W
Luquillo Experimental Forest (LUQ)	Puerto Rico	Jean Lodge	19°00′ N – 66°00′ W
Loch Vale Watershed (LVW)	Colorado	Jill Baron	40°17′ N – 105°39′ W
Monte Verde (MTV)	Costa Rica	Nalini Nadkarni	10°18′ N – 84°48′W
North Inlet (Hobcaw Barony) (NIN)	South Carolina	Jim Morris	33°30′ N – 79°13′ W
North Temperate Lakes (NLK)	Wisconsin	Tom Gower	46°00′ N – 89°40′ W
Niwot Ridge/Green Lakes Valley (NWT)	Colorado	Marilyn Walker	40°03′ N – 105°37′ W
Olympic National Park (OLY)	Washington	Robert Edmunds	47°50′ N – 122°53′ W
Santa Margarita Ecological Reserve (SMR)	California	James Reynolds	33°30′ N – 106°40′ W
Sevilleta National Wildlife Refuge (SEV)	New Mexico	Carl White	34°29′ N – 106°40′ W
University of Florida (UFL)	Florida	Henry Gholz	29°30 ′N – 82°15′ W
Virginia Coast Reserve (VCR)	Virginia	Linda Blum	37°30′ N – 75°40′ W

position are similar. We hypothesize that a general model of decomposition incorporating litter quality and climate can be developed which can adequately predict both above- and belowground decomposition. If this is not the case, the question remains as to whether or not differences between above- and belowground dynamics can be generalized or if they are ecosystem specific.

Hypothesis 4—Site-specific (ecosystem) effects on decomposition. Significant interactions occur between litter source or type and location. Some studies (e.g. Hunt *et al.* 1988) have suggested that decomposer communities may be specialized to litter types characteristic of a given ecosystem. For example, litter from temperate zone conifers might be expected to decompose more slowly in ecosystems that lack comparable species, independent of litter quality or climate.

Materials and methods

Litter collection, preparation and processing

Pinus resinosa leaf samples consisted of freshly fallen litter from mature trees collected on mesh screens,

between precipitation events, during periods of peak natural litterfall under mature forests at the Harvard Forest (HFR, Table 1). Fresh green leaves of *Drypetes* were harvested directly from trees in a Puerto Rican rain forests (LUQ). Live fine roots (< 2.0 mm diameter) were collected by excavation from the surface soil at a site in Florida (UFL, *P. elliottii*) and at LUQ (*Drypetes*); the Florida pine roots were all obviously ectomycorrhizal. All samples were air dried, then sent to a central processing laboratory at Oregon State University to be prepared and distributed to all of the LIDET sites. Litter was confined in mesh bags, each one 20×20 cm, and included either 5 g of fine roots or 10 g of leaves. The leaf bags had a 1-mm mesh nylon top and a 55 µm mesh DACRON cloth bottom (to reduce fragmentation losses), while the root bags were constructed completely of 55 µm mesh DACRON cloth. Initial moisture contents, oven-dry weights and chemistries were obtained from subsamples. A pilot study (Harmon, unpubl. data) found no effects of 1.0 vs. 5.0 mm mesh sizes on leaf decomposition, except at one desert site (JRN) where termites made off with some litter from the 5.0 mm bags. No similar evaluation of root bag effects was carried out. A caution thus

Table 2 Mean annual precipitation (MAP), mean annual temperature (MAT), actual evapotranspiration (AET), and ecosystem type for the LIDET sites (arranged alphabetically by Ecosystem type). DEFAC is a complex climatic factor related to decomposition as described by the CENTURY model

Site	MAP (mm)	MAT (°C)	AET (mm)	DEFAC	Ecosystem type	Forest type[1]
KBS	851	9.3	604	0.30	Agriculture	n
NWT	931	−3.7	234	0.10	Alpine tundra	n
ARC	284	−7.0	227	0.12	Arctic tundra	n
BNZ	260	−3.6	202	0.11	Boreal conifer forest	c
JUN	1367	4.4	530	0.15	Boreal conifer forest	c
LVW	1080	2.4	434	0.15	Boreal conifer forest	c
SEV	209	13.7	209	0.10	Desert	n
JOR	233	14.6	231	0.13	Desert	n
CDR	727	5.5	727	0.28	Grassland	n
CPR	310	8.7	299	0.19	Grassland	n
KNZ	835	12.7	790	0.41	Grassland	n
VCR	1076	14.2	979	0.43	Saltmarsh	n
NIN	1300	18.0	1284	0.55	Saltmarsh	n
CWT	1847	12.5	1015	0.35	Temperate broadleaf forest	b
HBR	1298	5.5	608	0.22	Temperate broadleaf forest	b
HFR	1120	6.8	564	0.24	Temperate broadleaf forest	b
AND	2291	9.3	552	0.15	Temperate conifer forest	c
NLK	792	4.4	548	0.22	Temperate conifer forest	c
OLY	2952	9.5	524	0.21	Temperate conifer forest	c
BSF	1121	14.5	363	0.18	Temperate conifer forest	c
UFL	1207	21.2	1205	0.55	Temperate conifer forest	c
GSF	700	22.5	150	0.18	Tropical dry forest	b
LBS	3914	25.6	1477	0.93	Tropical lowland rainforest	b
LUQ	3500	22.1	1139	0.71	Tropical montane rainforest	b
MTV	2685	17.6	622	0.45	Tropical montane rainforest	b
BCI	2615	25.6	1187	0.82	Tropical seasonal rainforest	b

[1]As used for testing Hypothesis 4 (b, broadleaved; c, conifer; n, neither)

remains regarding unknown potential mesh-size effects on the decomposition process in this study.

Litterbags were placed in the field during 1990 and 1991 at the peak of seasonal litterfall at four replicate locations at each site. In some cases (e.g. UFL), 'replications' were different geographical locations within the same forest type, soil type and environment, all within 50 km of each other. In other cases, a 'replication' was interpreted to mean subregional representation with several ecosystems included (e.g. four different forest types at BSF). In these contrasting cases, the variations around the mean values were relatively lower and higher, respectively. Leaf bags were placed flat on the top of the existing litter layer while root bags were buried with the top edge of the bag parallel with the surface of the mineral soil. All of the bags were then left undisturbed until they were removed for analysis.

Collection of the bags occurred once a year during the autumn at most sites. However, sites in the tropics made collections more frequently, sometimes using up five sets of bags in only one year, while less than five collections were made over the 5-y period at a few sites. Retrieved bags were opened locally and any extraneous materials obviously not derived from the initial litter source were removed. Litter was then weighed fresh, dried for at least 24 h at 55 °C, then reweighed dry. All the samples were then returned to Oregon State University for additional analyses.

The initial ash content and chemistry of leaves and roots were determined at Oregon State University. Analysis of organic constituent fractions followed the methods of McClaugherty *et al.* (1985) and Ryan *et al.* (1990). Non-polar extractives (i.e. soluble fats, waxes and oils) were removed using dichloromethane (Tappi 1976). Simple sugars and water-soluble phenolics (together referred to as water-soluble extractives) were removed with hot water (Tappi 1981). Simple sugars were determined with the phenol-sulphuric acid assay (Dubois *et al.* 1956). Water-soluble phenolics were determined using the Folin–Denis procedure (Allen *et al.* 1974). Lignin content was determined by hydrolysing extractive-free material with sulphuric acid and weigh-

Table 3 Average initial chemical composition of the four substrates used in this LIDET analysis (± 1 SD). An anova indicated that effects of both litter type (root, leaf) and species were significant at $P \leqslant 0.01$. WSE = water soluble extractives.

Species	Litter type	% Lignin	% N	Lignin:N	% WSE
Drypetes	leaf	10.91 ± 2.91	1.97 ± 0.08	5.45 ± 1.90	40.4 ± 1.3
Drypetes	fine root	16.13 ± 2.93	0.76 ± 0.11	19.69 ± 2.23	19.9 ± 2.9
Pinus	leaf	19.18 ± 10.12	0.59 ± 0.09	30.06 ± 19.73	20.6 ± 2.1
Pinus	fine root	34.90 ± 6.60	0.82 ± 0.12	41.42 ± 11.92	20.1 ± 2.0

ing the insoluble residue (Effland 1977). Ash content was determined by heating material in a muffle furnace at 450 °C for 8 h and weighing the residue. Nitrogen (N) content was determined using an Alp–Kem rapid flow analyser following microKjeldahl digestion. Initial C content was determined on a Carla–Erba NA-1500 Series 2 NCS analyser.

We also measured the ash content of decomposed samples to present the results on an ash-free basis. Two procedures were used to determine ash content. Approximately 20% of the samples had ash content determined using a muffle furnace as described above. The rest of the samples had ash content determined using near infrared reflectance spectroscopy (NIR) (Wessman *et al.* 1988; Bolster *et al.* 1996; Harmon & Lajta 1999). NIR predictions of ash content were based on calibration with the muffle furnace method. These predictions were corroborated against samples that had not been used as part of the calibration process.

Environmental data

Site-specific monthly environmental data were supplied by each co-operating investigator (Table 2). In most cases, the data supplied were multiyear averages from nearby standard meteorological stations (e.g. recording NOAA stations or NSF Long-term Ecological Research (LTER) sites). Actual evapotranspiration (AET) was estimated using monthly air temperature and precipitation (Thornthwaite & Mather 1947). Potential evapotranspiration (PET) was also tested, but did not provide many significant relationships and so was dropped from further analysis. A more complex synthetic climate variable, DEFAC, based on monthly local climate data was provided for each of the sites using the equations in the CENTURY model (Parton *et al.* 1994). DEFAC is calculated as the product of a temperature and a water-stress term. The temperature term, f_t, is defined as $0.08^*\exp(0.095^*T_{soil})$, where T_{soil} is the soil temperature, and the water stress term, f_w, as $1.0/(1.0 + 30 \times \exp(-8.5^*w_{rat}))$, where w_{rat} is the ratio of rainfall plus stored water to the potential evaporation rate (Parton *et al.* 1993). Potential evapotranspiration is calculated using equations from Linacre (1987) as a function of average monthly maximum and minimum air temperature. DEFAC varies from 0 to 1 and represents the relative climatic controls over decomposition in CENTURY.

Statistical analyses

The basis for our analyses is the negative exponential decay constant (k), derived using the model of Olson (1963) for individual sites, species and litter types:

$$y = e^{-kt}, \qquad (1)$$

where y is the fraction of mass remaining at some time, t (years). To test specific hypotheses, we used three derived variables from these individual decay models, and related them to environmental variables across all the sites using regression analysis and/or analysis of variance (anova). The first variable is the k-value for each species and/or litter type, or k-values variously averaged over species and litter type for each site. The second is the predicted mass remaining at the end of 5 years from the exponential decay models, using this instead of actual data points at 5 years to smooth out random variation in year-to-year observations. Finally, we predicted the length of Phase I, defined as the time (y) to 20% mass remaining (after Aber *et al.* 1990). All mass loss estimates were calculated on an ash-free basis.

Results and discussion

Initial chemical characteristics of the litter

The four substrates in this study contrasted highly in terms of their initial chemical compositions (Table 3). The closest values were for root N concentrations (0.76 vs. 0.82%), although in this case the *Drypetes* roots had less than half the lignin concentrations of the pine. *Drypetes* roots and pine leaves had similar lignin concentrations (16 vs. 19%), but their N concentrations differed substantially. The N concentration of *Drypetes* roots was less than half of the concentration in the leaves, while the pine roots had a N concentration 40% greater than that of pine leaves. The greatest relative differences among the litters were the very high initial N concentration of the *Drypetes* leaves (1.97%), and the high initial lignin

Table 4 Decomposition constants (*k*-values) and the associated R^2s from negative exponential regression equations of fractional mass remaining related to time, and estimated lengths of Phase 1 and fractions of mass remaining at 1 y and 5 y for each LIDET site, species and litter type. DRGL, *Drypetes glauca*; PIEL, *Pinus elliottii*; PIRE, *Pinus resinosa*. Arranged alphabetically on site acronym.

Site	Species	Type	*k*	R^2	Length of Phase 1 (y)	Fractional mass remaining at 1 y	5 y
AND	DRGL	Leaves	0.300	0.85	4.508	0.573	0.173
	DRGL	Roots	0.241	0.97	6.384	0.731	0.279
	PIEL	Roots	0.131	0.95	11.787	0.818	0.485
	PIRE	Leaves	0.183	0.98	8.797	0.834	0.401
ARC	DRGL	Leaves	0.163	0.83	8.772	0.707	0.369
	DRGL	Roots	0.077	0.75	19.356	0.825	0.606
	PIEL	Roots	0.038	0.62	40.346	0.891	0.765
	PIRE	Leaves	0.064	0.92	24.584	0.899	0.696
BCI	DRGL	Leaves	3.734	0.79	0.486	0.029	0.000
	DRGL	Roots	0.980	0.90	1.444	0.309	0.006
	PIEL	Roots	0.494	0.94	3.120	0.570	0.079
	PIRE	Leaves	0.467	0.95	3.481	0.637	0.098
BNZ	DRGL	Leaves	0.129	0.81	11.330	0.759	0.453
	DRGL	Roots	0.127	0.94	12.257	0.831	0.501
	PIEL	Roots	0.059	0.73	25.733	0.853	0.675
	PIRE	Leaves	0.062	0.86	25.272	0.907	0.707
BSF	DRGL	Leaves	0.196	0.79	7.327	0.689	0.315
	DRGL	Roots	0.175	0.90	8.587	0.756	0.375
	PIEL	Roots	0.068	0.63	22.210	0.850	0.647
	PIRE	Leaves	0.047	0.96	34.046	0.952	0.788
CDR	DRGL	Leaves	0.224	0.81	6.031	0.617	0.252
	DRGL	Roots	0.343	0.97	4.681	0.708	0.179
	PIEL	Roots	0.086	0.71	16.900	0.790	0.559
	PIRE	Leaves	0.164	0.95	9.936	0.862	0.448
CPR	DRGL	Leaves	0.205	0.99	7.741	0.798	0.351
	DRGL	Roots	0.237	0.96	6.665	0.764	0.297
	PIEL	Roots	0.152	0.99	10.531	0.855	0.465
	PIRE	Leaves	0.100	0.97	16.238	0.918	0.615
CWT	DRGL	Leaves	0.407	0.30	3.065	0.463	0.091
	DRGL	Roots	0.300	0.91	4.906	0.644	0.194
	PIEL	Roots	0.131	0.89	11.551	0.793	0.470
	PIRE	Leaves	0.264	0.98	5.916	0.732	0.255
GSF	DRGL	Leaves	0.362	0.75	3.685	0.528	0.124
	DRGL	Roots	0.392	0.75	3.815	0.602	0.126
	PIEL	Roots	0.190	0.68	8.061	0.766	0.358
	PIRE	Leaves	0.143	0.78	11.391	0.884	0.499
HBR	DRGL	Leaves	0.382	0.78	3.217	0.466	0.101
	DRGL	Roots	0.225	0.92	6.521	0.694	0.282
	PIEL	Roots	0.110	0.91	13.771	0.820	0.527
	PIRE	Leaves	0.287	0.97	5.698	0.771	0.244
HFR	DRGL	Leaves	0.395	0.81	3.167	0.471	0.097
	DRGL	Roots	0.208	0.90	6.971	0.692	0.301
	PIEL	Roots	0.103	0.85	14.595	0.808	0.536
	PIRE	Leaves	0.269	0.99	6.063	0.781	0.266
JRN	DRGL	Leaves	0.233	0.87	6.275	0.684	0.269
	DRGL	Roots	0.264	0.97	5.977	0.745	0.259
	PIEL	Roots	0.065	0.72	23.287	0.844	0.652
	PIRE	Leaves	0.229	0.96	7.352	0.857	0.343

Table 4 (Continued)

Site	Species	Type	k	R^2	Length of Phase 1 (y)	Fractional mass remaining at	
						1 y	5 y
JUN	DRGL	Leaves	0.447	0.96	3.394	0.584	0.097
	DRGL	Roots	0.299	0.99	5.402	0.747	0.226
	PIEL	Roots	0.143	0.97	11.068	0.846	0.477
	PIRE	Leaves	0.224	0.89	7.469	0.854	0.348
KBS	DRGL	Leaves	0.961	0.51	2.048	0.548	0.012
	DRGL	Roots	0.133	0.47	9.187	0.593	0.349
	PIEL	Roots	0.119	0.62	12.027	0.743	0.461
	PIRE	Leaves	0.072	0.54	20.089	0.789	0.592
KNZ	DRGL	Leaves	0.235	0.98	6.739	0.771	0.301
	DRGL	Roots	0.233	0.81	6.021	0.646	0.254
	PIEL	Roots	0.105	0.91	14.614	0.831	0.547
	PIRE	Leaves	0.146	0.98	11.193	0.885	0.494
LBS	DRGL	Leaves	0.495	0.33	0.820	0.183	0.025
	DRGL	Roots	0.593	0.92	2.268	0.424	0.040
	PIEL	Roots	0.340	0.96	4.370	0.630	0.161
	PIRE	Leaves	0.395	0.87	3.701	0.581	0.120
LUQ	DRGL	Leaves	1.209	0.55	0.611	0.125	0.001
	DRGL	Roots	0.919	0.95	1.656	0.366	0.009
	PIEL	Roots	0.501	0.82	3.042	0.557	0.075
	PIRE	Leaves	0.624	0.96	2.533	0.521	0.043
LVW	DRGL	Leaves	0.213	0.79	6.834	0.694	0.296
	DRGL	Roots	0.184	0.95	8.393	0.778	0.373
	PIEL	Roots	0.055	0.54	27.278	0.859	0.688
	PIRE	Leaves	0.032	0.56	47.919	0.918	0.806
MTV	DRGL	Leaves	0.403	0.48	2.100	0.311	0.062
	DRGL	Roots	0.463	0.93	3.049	0.516	0.081
	PIEL	Roots	0.347	0.99	4.621	0.702	0.175
	PIRE	Leaves	0.224	0.98	7.201	0.801	0.327
NIN	DRGL	Leaves	1.744	0.93	0.785	0.137	0.000
	DRGL	Roots	0.112	0.70	12.807	0.750	0.479
	PIEL	Roots	0.120	0.76	11.997	0.749	0.463
	PIRE	Leaves	0.595	0.94	2.651	0.534	0.049
NLK	DRGL	Leaves	0.415	0.95	3.718	0.619	0.117
	DRGL	Roots	0.223	0.90	6.992	0.762	0.312
	PIEL	Roots	0.150	0.99	10.671	0.852	0.468
	PIRE	Leaves	0.145	0.99	11.046	0.862	0.482
NWT	DRGL	Leaves	0.144	0.81	9.982	0.729	0.410
	DRGL	Roots	0.088	0.77	16.804	0.805	0.566
	PIEL	Roots	0.036	0.41	40.913	0.856	0.740
	PIRE	Leaves	0.047	0.93	33.763	0.928	0.769
OLY	DRGL	Leaves	0.443	0.84	2.878	0.460	0.078
	DRGL	Roots	0.219	0.87	6.519	0.669	0.279
	PIEL	Roots	0.127	0.87	11.686	0.781	0.469
	PIRE	Leaves	0.200	0.91	7.456	0.729	0.327
SEV	DRGL	Leaves	0.118	0.55	12.382	0.763	0.476
	DRGL	Roots	0.284	0.99	5.557	0.729	0.234
	PIEL	Roots	0.095	0.93	16.506	0.870	0.595
	PIRE	Leaves	0.146	0.91	11.148	0.883	0.492

Table 4 (Continued)

Site	Species	Type	k	R^2	Length of Phase 1 (y)	Fractional mass remaining at 1 y	Fractional mass remaining at 5 y
UFL	DRGL	Leaves	0.313	0.71	3.728	0.470	0.134
	DRGL	Roots	0.289	0.86	4.805	0.601	0.189
	PIEL	Roots	0.165	0.92	9.174	0.770	0.398
	PIRE	Leaves	0.227	0.90	6.667	0.724	0.292
VCR	DRGL	Leaves	1.471	0.99	1.111	0.235	0.001
	DRGL	Roots	0.074	0.62	19.621	0.791	0.589
	PIEL	Roots	0.051	0.46	28.734	0.818	0.667
	PIRE	Leaves	0.303	0.96	5.418	0.762	0.227

Table 5 Pearson correlation coefficients between the main LIDET climate variables. All correlations were significant at $P = 0.0001$

	MAP	MAT	AET
DEFAC	0.71	0.72	0.90
MAP	—	0.45	0.65
MAT	—	—	0.60

Fig. 1 The best predictor of the site mean k-value was a quadratic relationship using DEFAC from the CENTURY model.

concentration of the pine roots (34.90%). The contrasts in lignin and N concentrations were magnified in the lignin:N ratios, which consequently ranged from 5.45 to over 41.

Notably, the concentrations of water-soluble extractives (WSE) were virtually identical for three of the four litters. Only leaves of *Drypetes* were significantly different, with concentrations double those of the other litters.

Decomposition parameters

Averages from the four replications at each site were used for all the analyses in this paper. The number of data points over the five years for each site ranged from three to 10, reflecting both the range in decomposition rates and the variable frequency of sampling across the LIDET sites.

All of the negative exponential regressions for the separate sites, species and litter types were significant at probability (P) levels of ≤ 0.15, and half of the regression R^2s were higher than 0.90 (Table 4). The poorest fits were generally for pine roots, although this was not always the case. The high degree of success of fitting the exponential model was an important initial result of these analyses and suggested that there may in fact be general factors controlling decomposition across these ecosystems. The resulting k-values (Table 4) ranged from 0.032 (at LVW for pine leaves) to 3.734 (at BCI for *Drypetes* leaves).
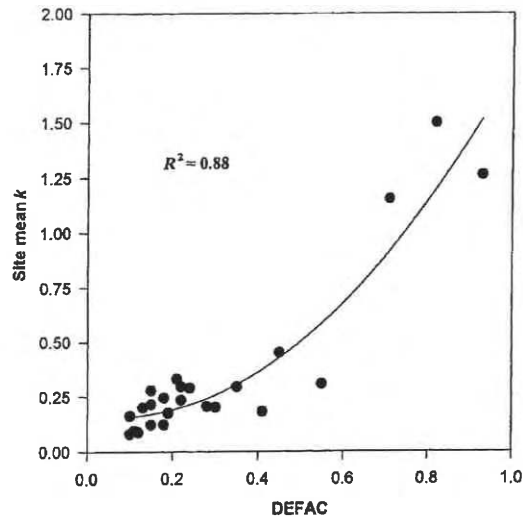
The end of Phase 1 was not reached in many cases by the end of the five years, so that long-term dynamics cannot be uniformly addressed empirically across the LIDET sites with this dataset. However, Aber *et al.* (1990) determined that extrapolations of exponential models are generally valid until the end of Phase 1. Therefore, we used the individual negative exponential models to predict the time it would take to reach the end of Phase 1, if decomposition had in fact not proceeded that far. Modelled Phase 1 lengths ranged from 0.49 years (at BCI for *Drypetes* leaves) to 47.92 years (at LVW for pine leaves) (Table 4).

Modelled fractions of mass remaining after one year ranged from 0.029 (at BCI for *Drypetes* leaves) to 0.952 (at BSF for pine leaves). The lowest and highest modelled mass remaining fractions at five years were 0.000 (at BCI

Table 6 (a) Best linear models ($y = a + bx$) and (b) best quadratic models ($y = a + bx + cx^2$) of decomposition as related to climate in the LIDET study, based on R^2 (root regressions excluded the two saltmarsh sites, VCR and NIN).

variable	a	b	c	x	R^2	p level
(a) Best linear models ($y = a + bx$)						
Drypetes leaves						
Fraction of mass remaining at 5 y						
	0.3576	−0.0003	—	AET	0.50	0.0001
Length of Phase 1	8.8639	−0.0064	—	AET	0.54	0.0001
k	−0.0816	2.1216	—	DEFAC	0.41	0.0005
Drypetes roots						
Fraction of mass remaining at 5 y						
	0.4215	−0.0146	—	MAT	0.76	0.0001
Length of Phase 1	10.8958	−0.3771	—	MAT	0.68	0.0011
k	0.0717	0.7963	—	DEFAC	0.66	0.0001
Pine leaves						
Fraction of mass remaining at 5 y						
	0.7064	−0.0005	—	AET	0.5955	0.0001
Length of Phase 1	20.8676	−0.7082	—	MAT	0.3144	0.0029
k	0.0139	0.0003	—	AET	0.5971	0.0001
Pine roots						
Fraction of mass remaining at 5 y						
	0.6889	−0.6978	—	DEFAC	0.71	0.0001
Length of Phase 1	24.3687	−0.8410	—	MAT	0.59	0.0001
k	0.0163	0.4718	—	DEFAC	0.71	0.0001
(b) best quadratic models ($y = a + bx + cx^2$)						
Drypetes leaves						
Fraction of mass remaining at 5 y						
	0.4750	−0.0007	2.8×10^{-7}	AET	0.56	0.0001
Length of Phase 1	11.2800	−0.0152	5.8×10^{-6}	AET	0.60	0.0001
k	−0.1592	2.6286	−0.5494	DEFAC0.41	0.0024	
Drypetes roots						
Fraction of mass remaining at 5 y						
	0.4278	−0.0191	0.0002	MAT	0.78	0.0001
Length of Phase 1	11.4226	−0.6990	0.0148	MAT	0.79	0.0001
k	0.1188	0.4833	0.3320	DEFAC0.67	0.0001	
Pine leaves						
Fraction of mass remaining at 5 y						
	0.7235	−0.0005	4.1×10^{-8}	AET	0.60	0.0001
Length of Phase 1	21.6913	−1.1854	0.0222	MAT	0.35	0.0072
k	0.0635	0.0001	-1.2×10^{-7}	AET	0.61	0.0001
Pine roots						
Fraction of mass remaining at 5 y						
	0.7538	−1.1297	0.4581	DEFAC	0.72	0.0001
Length of Phase 1	24.4501	−1.5015	0.0304	MAT	0.67	0.0001
k	0.0162	0.4722	−0.0004	DEFAC	0.71	0.0001

and NIN for *Drypetes* leaves) and 0.806 (at LVW for pine leaves), respectively.

Some LIDET results can be compared with previously published data for the same species. For example, on similar and nearby sites to the current LIDET site in Florida, Gholz *et al.* (1985) found a linear decay rate for *P. elliottii* needles of 15% per year averaged over 2 years, whereas the current data (Table 4) indicate a slightly higher rate of 18% per year for *P. resinosa* (also averaged

over 2 years). Gholz *et al.* (1986) found that *P. elliottii* roots ≤ 2 mm in diameter decayed at a linear rate averaging 10% per year over two years; the current results suggest a somewhat higher rate of 14% per year. However, even such direct comparisons are problematic as, for example, the needles in Gholz *et al.*'s (1985 and 1986) studies had significantly lower N concentrations (and given that they were of two different species, perhaps different concentrations of other chemicals as well), the root samples
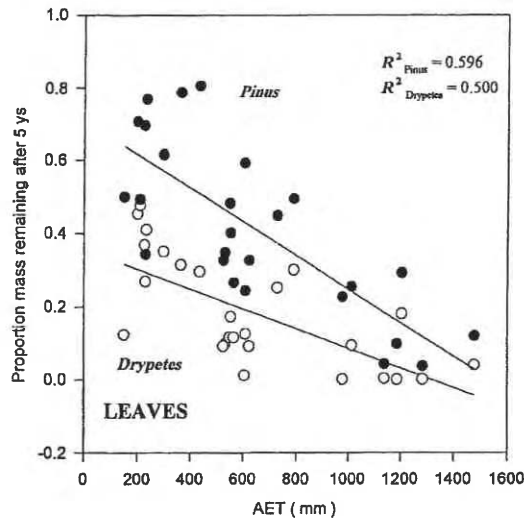
Fig. 2 Relationship between the proportion of mass remaining after 5 years and AET for leaves decomposing at the LIDET sites. Lines are linear least-squares fits. Both regressions are significant at $P = 0.0001$.
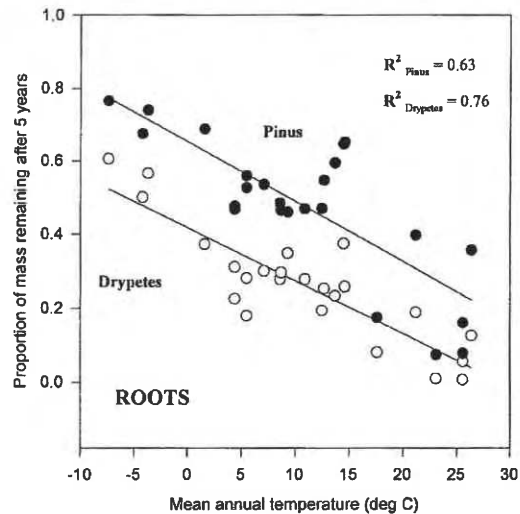

Fig. 3 Relationship between the proportion of mass remaining after 5 y and MAT for fine roots decomposing at the LIDET sites. Lines are linear least-squares fits. The two saltmarsh sites have been excluded in this analysis. Both regressions are significant at $P = 0.0001$.

(although of the same diameter) were buried horizontally in the soil in the earlier study, the stands used were not the same, and environmental conditions may have been significantly different during the two studies. In spite of the differences in experimental conditions, however, the average values are within 20% of each other for pine needles and 30% for pine roots in the various studies.

Berg & Ågren (1984) reported the pattern of decomposition of *Pinus sylvestris* needle litter over five years in Sweden. Their average *k*-value, calculated in the same manner as in this study, was 0.286 per years, very close to that observed for pine leaf decomposition at HFR (0.269) and HBR (0.287) (Table 4), two northeastern U.S. forest sites with climates similar to that of the site in Sweden.

Climate effects—testing Hypothesis 1

Given the initial anova results, simple linear regressions were next developed for each species and litter type across all sites to explore the relationship between decomposition and environment. The independent variables used were AET, mean annual temperature (MAT), mean annual precipitation (MAP), and DEFAC for each site.

To some extent the climatic variables are inter-related (Table 5). AET and DEFAC are highly correlated ($r = 0.90$). The correlations of AET with MAT and MAP are 0.60 and 0.65, respectively. The correlation of DEFAC with MAT is 0.72 and with MAP is 0.71. In other words, MAT and MAP influence DEFAC to a similar degree.

AET has been used extensively to predict NPP and weights moisture availability more severely than DEFAC. In contrast, DEFAC places a primary emphasis on temperature over a relatively broad range of moisture availability, and still maintains some decomposition at very low precipitation. This is consistent with our results from desert ecosystems and earlier conclusions by Whitford *et al.* (1981) suggesting that decomposition is less restricted by low-moisture conditions than primary production.

Scatterplots between the mean *k*-values for each site (i.e. averaged over species and tissues) and individual climatic variables tended to be nonlinear. Assuming quadratic relationships, MAT and MAP were similar predictors of *k* ($R^2 = 0.55$ for both). AET provided a better quadratic fit ($R^2 = 0.66$), while the best fit was provided using DEFAC ($R^2 = 0.88$, Fig. 1); the slope of the relationship was less steep for DEFAC than for AET. When the relationships were linearized with a ln-transformation of *k*, the results were similar, with the best fit using DEFAC ($R^2 = 0.77$) followed by AET ($R^2 = 0.65$), MAT ($R^2 = 0.57$) and MAP ($R^2 = 0.55$).

Best linear and quadratic models for each species and litter type as related to climate are provided in Table 6 (a) and (b). Removing roots from the two saltmarsh sites from the regressions resulted in substantial increases in belowground R^2s. Roots of both *Drypetes* and pine at VCR were outliers in every case, with consistently lower *k*-values, longer lengths of Phase 1 and more mass remaining after 5 years. In contrast, leaves of both species
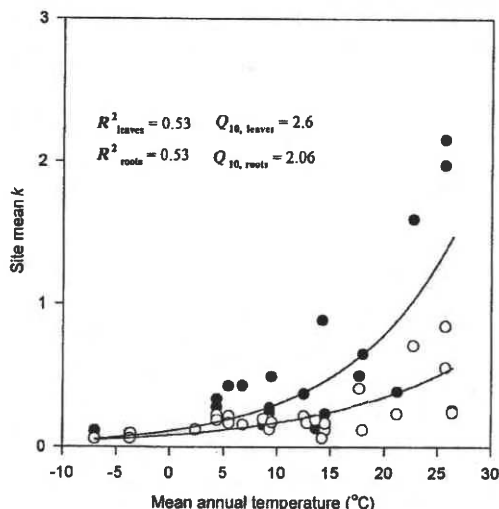
Fig. 4 Relationship between the mean k-values for each LIDET site and MAT. Q_{10} values were obtained from the quadratic least-squares regression curves fit as indicated. Both regressions were significant at $P = 0.0001$.

Table 7 Ratios of *Drypetes* k-values to pine k-values (averaged over litter type) across 10 ecosystem types in LIDET

Ecosystem type (# of LIDET sites)	Ratio of k for high (*Drypetes*)/ low (pine) quality litter
Agriculture (1)	5.76
Saltmarsh (2)	3.89
Boreal Conifer Forest (3)	2.89
Tundra (2)	2.56
Tropical Wet Forest[1] (4)	2.45
Tropical Dry Forest (1)	2.20
Temperate Conifer Forest (5)	2.14
Grassland (3)	1.97
Desert (2)	1.68
Temperate Broadleaf Forest (3)	1.66

[1]lowland, montane and seasonal tropical forests combined from Table 2

at this site followed the regression trends closely, which indicates very different controls over above- and below-ground decomposition at this coastal dune site, while decomposition patterns remained consistent between the species. The fact that the nearby estuary site, NIN, also had higher lengths of Phase 1 and mass remaining at 5 years for roots of both species supports the contention that factors other than MAT control belowground disappearance of roots at both coastal sites. These sites were atypical compared to the other 26 sites, in that the belowground litter bags were placed in generally anaerobic conditions in loose sandy soils, with brackish water, and had correspondingly low decomposition rates.

To illustrate general trends with climate, we plotted the proportion of mass remaining after 5 years as a function of AET, the best linear predictor for leaves of the two species (Fig. 2), and MAT, the best predictor (along with DEFAC) for roots (Fig. 3, excluding saltmarsh roots). The consistent differences between species (*Drypetes* > pine) across the sites is most obvious from Fig. 3. Differences between the litters of each species are not large, but are still consistent, with leaves decaying more rapidly than roots across sites.

The two warm desert sites (SEV and JRN) also deviated substantially in a number of cases. However, at SEV it was only *Drypetes* leaves that departed from the regressions, while at JRN it was only pine roots, with decomposition relatively slow in both cases compared to

the regression trends. However, further examination of data from these two ecosystems did not support a consistent pattern of departure for warm deserts, nor did the additional results from the slightly wetter and cooler CPR, or the dryer but warmer GSF.

Decomposition of pine roots at BSF was also lower and slower than expected, although the predicted length of Phase 1 was average. In a few other cases, one type of litter departed from the trends, but there was no consistency in the departures. For example, the mass remaining after 5 years for pine leaves at both HBR and HFR was lower than expected, the two low-elevation wet tropical sites had higher k-values for *Drypetes* leaves than predicted, and the k-value for *Drypetes* leaves at GSF was relatively low. But, in no case were there corresponding inconsistencies in other relationships, suggesting random experimental errors (such as mismeasurement, unnoticed effects of detritivory, mechanical disturbances, etc.) or unexplainable natural variation.

Using a plot of site mean k-values for roots and leaves as a function of MAT, Q_{10} values can be extracted for each litter type. Results indicated a Q_{10} of 2.05 for roots and 2.70 for leaves (Fig. 4). The root value is right on the expected value of 2.0 for chemical and enzymatic reactions and a wide range of observations of plant and soil respiration (e.g. Ryan *et al.* 1994; Lavigne *et al.* 1997). The leaf value is higher than expected and observed for live foliar respiration, but is within the literature range reported for other tissues (Amthor 1984; Ryan 1991).

Substrate quality effects—testing Hypothesis 2

The higher decomposition rates and the stronger effect of MAP for *Drypetes* leaves may be due to their consider-

Table 8 Results of the 3-way anova for testing Hypothesis 3, focusing on the ratio of *k*-values for above-ground litter (leaves) vs. belowground litter (roots) (averaged over species) across ecosystem types (i.e. the ecosystem–tissue interactions).

Ecosystem type	Ratio aboveground *k*/ belowgound *k*
Saltmarsh	11.53
Agriculture	4.10
Temperate Broadleaf Forest	1.86
Tundra	1.74
Tropical Wet Forest	1.63
Temperate Conifer Forest	1.38
Boreal Conifer Forest	1.28
Desert	1.03
Grassland	0.93
Tropical Dry Forest	0.87

ably higher WSE fraction (40% on a dry mass basis) in contrast to the *Drypetes* roots and both roots and leaves of pine (Table 3). Many decomposition models (e.g. Moorhead *et al.* 1999) represent this fraction explicitly in their model structures and have demonstrated the importance of the fraction in predicting rates of mass loss from litter decomposition. Parton *et al.* (1994) have shown that the water-soluble extractive fraction of litter decreases with increasing lignin:N ratio of the litter and that individual species have quite different partitioning of litter into the water-soluble extractive, lignin and cellulose fractions. Because tissues of plants characteristic of different ecosystem types and different climate zones differ sharply in water-soluble concentrations, this variable may well play an important role in the construction of general models of decomposition at global scales. In the LIDET case, *Drypetes* leaves did decompose more rapidly than the other substrates, but WSE concentrations cannot explain the other differences observed.

We used a 3-way anova to look at ecosystem × species interactions, with *k*-values as the response variable, ecosystem type, species and tissue as the main effects, and 2-way terms for the interactions between ecosystem type and species, and ecosystem type and tissue. We collapsed the 25 LIDET sites from Table 2 into 10 ecosystem types to make generalizations possible, then focused on the ecosystem–species interaction, calculating the ratio of the *k*-values for *Drypetes* to the *k*-values for pine at each site (averaging over leaves and roots) (Table 7).

Results of the anova indicated that the three main effects were each highly significant ($P = 0.0001$, 0.0015 and 0.0153 for ecosystem, species and tissue, respectively). However, neither interaction term was significant (species × ecosystem $P = 0.3400$ and ecosystem–tissue

interaction $P = 0.1500$). These results strongly support the grouping of ecosystems that we used, and highlight once again the dominant influence of both species and tissue on decomposition. However, they also indicate that there were no consistent trends for either tissue of either species to decay more or less rapidly in relation to this ecosystem grouping.

Because of the scope of LIDET in time and space, direct comparisons with other studies or models of decomposition are difficult to make without extrapolations. Meentemeyer (1978, 1984) utilized data from five sites ranging from the south-eastern U.S. to Norway, covering an AET range from 343 to 797 mm, to develop a model of leaf decomposition which utilizes AET and initial lignin concentration as independent variables and predicts mass loss after one year. In order to compare our results with this model at the lignin concentrations in Table 3, we derived simple linear regressions of leaf mass remaining after one year as a function of AET (data not shown). We then compared the results with the Meentemeyer model over the LIDET range of sites. The models showed good agreement for *Drypetes* leaf decomposition over the entire LIDET AET range, with the LIDET model slightly underestimating one-year mass loss at low AETs and overestimating at higher AETs, relative to the Meentemeyer model. However, the LIDET model predicted much lower pine leaf decomposition over almost the entire AET range, with the deviation increasing greatly as the Meentemeyer model was extrapolated to the higher LIDET AET values. Clearly extrapolating the Meentemeyer model to higher AET sites is not appropriate for the lower quality pine litter. Significantly, Meentemeyer's model overestimated decomposition for both *Drypetes* and pine leaves at the UFL and LBS LIDET sites, two sites whose only similarity is high AET. Previous underestimation of leaf decomposition in desert ecosystems using the Meentemeyer model was noted by Whitford *et al.* (1981) and Schaefer *et al.* (1985), although the LIDET results do not support this conclusion.

Our results generally support the trends reported by Aerts (1997). For example, again using AET as the independent variable, predicted *k*-values (from a linear model) for *Drypetes* and pine at 300 and 2000 mm AET (the minimum and maximum in Aert's fig. 1), indicate that our pine leaves are very near the slowest decomposing substrate included in his analysis, while *Drypetes* leaves are higher than his average ($k = 0.61$ and 2.19 for pine and *Drypetes*, respectively, vs. a mean of 1.91 from Aerts at an AET $= 2000$ mm y^{-1}). However, this comparison is made using *k*-values derived from 5 y of LIDET data compared with 1 y of data in Aerts, which assumes that climate controls over decomposition remain the same over time.

Table 9(a) Results of the anova used for examining site-specific (i.e. broadleaf vs. conifer from Table 1) effects on leaf decomposition in forest ecosystems.

Effects	F-value	P-value
Forest type	0.04	0.842
Species	3.45	0.075
AET	1.86	0.185
Species × Forest type	1.08	0.309
AET × Forest type	0.70	0.412

Table 9(b) Rates of decomposition (expressed as normalized k-values) for *Drypetes* and *Pinus* leaf litters in contrasting forest types

Treatment	Forest type	Least-square mean value for k
Drypetes	broadleaf	1.37
	conifer	0.426
Pinus	broadleaf	0.129
	conifer	0.188

Meentemeyer (1984) generalized that litter quality does not matter much where overall climate strongly constrains decomposition (e.g. in the Arctic). Our results do not support this. In contrast with Meentmeyer's hypothesis, the relative decomposition rates of high- and low-quality litter differ more in boreal forest or tundra than in broadleaf forest or grassland (Table 7). Our interpretation of Table 7 is that sites with higher moisture availability had higher ratios (including the low-precipitation boreal BNZ site and the two tundra sites, all due to low AET). This may reflect variation in microbial communities, or could be something as simple as variable leaching losses due to the highest quality litter (*Drypetes* leaves) having a very high WSE fraction. Because 'high quality' litters generally have high WSE fractions, this again argues for the inclusion of an initial leaching phase into decomposition models. The reason(s) for the very low ratio for temperate broadleaf forests (comparable to that of the deserts) is not clear at this time, but obviously deserves further attention.

Above- vs. belowground dynamics—testing Hypothesis 3

We used the same 3-way anova as above to test Hypothesis 3, but this time examined the ecosystem-tissue interaction. This is central to determining whether the relative difference between above- and belowground decomposition is consistent across sites. We hesitate to interpret the absolute differences between above- and belowground decomposition, as the roots and leaves were placed in different positions. However, because the same substrates were used at all locations, their relative performance can provide important insights.

The average k for leaves at all sites was 0.40, while for roots it was 0.24 (averaging across pine and *Drypetes*). We computed the ratio of the average k for aboveground decomposition to the average k for belowground decomposition in each ecosystem type (Table 8). Again, the obvious outlier was saltmarsh, with almost 12 times faster aboveground decomposition (i.e. 11.5 times higher k). The lone agricultural site (KBS) had more than double

the ratio of the next highest site (4.10 vs. 1.86), while the remaining values were all between 0.83 and 1.86.

Also notable (e.g. by comparing Figs 2 and 3 or R^2 values in Table 6) is the much lower scatter around the root relationships as compared to those for leaves. These results suggest that belowground environments exert a more consistent control over decay rates than aboveground environments; this is not surprising given the more constant nature of surface-soil microclimates than those of the litter layer (e.g. lower diurnal and seasonal fluctuations in temperature).

For grassland, tropical dry forest and desert, aboveground decomposition was slower than expected, given overall climate (aboveground:belowground ratios < 1.0). These ecosystems all have high solar radiation levels at or near the soil surface for much of the year, and higher temperature, lower humidity, and/or high UV radiation might contribute to a relatively hostile microclimate for aboveground litter decomposers. These ecosystems are all also prone to fire, which is likely the more important oxidizer of surface litter under natural conditions than microbes. The magnitude of the differences in Table 8 suggests that above- and belowground decomposition rates may need to be modelled separately, although exceptions to a more generalized model may be relatively minor and predictable.

Site-specific effects—testing Hypothesis 4

To some degree, Hypotheses 2 and 4 are confounded. Some studies have suggested that decomposer communities may be specialized to litter types characteristic of a given ecosystem (Hunt et al. 1988). If so, then significant interactions should occur between litter source or type and location. To state it in simple terms: Is there evidence in the LIDET data of a 'home field advantage'?

To test this, we restricted the data to aboveground (leaf) litter and categorized the sites (Table 2) as either conifer forest ($n = 8$), broadleaf forests ($n = 8$) or non-forests ($n = 10$), with the latter excluded from this test. Using PROC GLM in SAS (SAS 1996), we then looked for controls on k as a function of the main effects of forest type (conifer vs. broadleaf), species (*Drypetes* vs. pine)

and AET (as a representative climate variable), along with the species × forest-type interaction, and the AET × forest-type interactions (Table 9a). This analysis suggests that decomposition in the two forest types is not different ($P = 0.842$), and that pine and *Drypetes* litters are different (although the contrast is significant only at a $P = 0.075$ level). Interestingly, neither AET nor the species–forest interaction were significant.

Then, using the least-squares procedure to standardize the means of k-values for the midpoint of the continuous AET variable, we contrasted rates of decomposition of the litters of the two species in conifer and broadleaf habitats (Table 9b). On average, *Drypetes* litter decomposed 10.6 times faster than pine litter in broadleaf forests (1.37 vs. 0.13), while only 2.3 times faster than pine litter in conifer forests (0.426 vs. 0.188). This is strong evidence of a 'home field advantage', at least for *Drypetes* leaf litter; the effect was in a similar direction, but much smaller in magnitude for pine leaf litter, explaining the negative overall statistical significance in Table 9a. Given these results, litter from broadleaved trees would be expected to decompose more slowly in ecosystems that lack comparable plant and associated microbial species, independent of climate.

Conclusions

The LIDET study provided an opportunity to contrast the long-term (5-y) patterns of decomposition of clearly different tree litters over an unprecedented range of global climatic conditions. Several key results emerged from this analysis.

I Pine litter decomposed more slowly (based on k-values, mass remaining after 5 y, and lengths of Phase 1) than *Drypetes* litter, supporting the notion of strong control of substrate quality over decomposition rates.
II Climate exerts strong and consistent effects on decomposition. Neither MAT nor MAP alone explained the global pattern of decomposition; variables including both moisture availability and temperature (i.e. AET and DEFAC) were generally more robust than single variables. Across the LIDET range, decomposition of fine roots exhibited a Q_{10} of 2, while leaf decay had a higher value and exhibited greater variation.
III In general, roots decomposed more slowly than leaves, regardless of genus. However, the ratio of above- to belowground decomposition rates differed sharply across ecosystem types.
IV Broadleaf (*Drypetes*) litter decomposed much more rapidly than pine litter in 'broadleaved habitats' than in 'conifer habitats', evidence for a 'home-field advantage' for this litter.

While points I and II suggest that relatively simple models can predict decomposition based on litter quality and regional climate, points III and IV highlight ecosystem-specific problems that may introduce considerable error to such models. For example, point III suggests that general decomposition models based on above-ground litter quality and climate may significantly over- or underestimate belowground decomposition in specific ecosystems. Because of the immense carbon stores associated with detritus and soil organic matter, even small differences in predicted decomposition rates may have significant effects on estimated global C pools. Whether or not ecosystem-specific differences in the ratio of above- and belowground competition, the 'home-field advantage' effect, or other related issues need to be incorporated into global production/decomposition models, will depend on the magnitude of these effects relative to other sources of error.

This year (2000) will conclude 10 years of LIDET field collections. Opportunities will then exist to analyse and synthesize these data and to develop, as appropriate, more complex data-based models containing interactions of climate, substrate quality in a more continuous manner, and litter type (roots/leaves). While we have a very good sense of climate variability at the global scale, the same cannot be said about leaf and root litter amounts and quality. In order to estimate the contributions of root and leaf decomposition to the global carbon budget, such information must be obtained and then coupled with generalizable models of decomposition.

Acknowledgements

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