

# Cross-biome transplants of plant litter show decomposition models extend to a broader climatic range but lose predictability at the decadal time scale

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## Abstract

We analyzed results from 10-year long field incubations of foliar and fine root litter from the Long-term Intersite Decomposition Experiment Team (LIDET) study. We tested whether a variety of climate and litter quality variables could be used to develop regression models of decomposition parameters across wide ranges in litter quality and climate and whether these models changed over short to long time periods. Six genera of foliar and three genera of root litters were studied with a 10-fold range in the ratio of acid unhydrolyzable fraction (AUF, or 'lignin') to N. Litter was incubated at 27 field sites across numerous terrestrial biomes including arctic and alpine tundra, temperate and tropical forests, grasslands and warm deserts. We used three separate mathematical models of first-order (exponential) decomposition, emphasizing either the first year or the entire decade. One model included the proportion of relatively stable material as an asymptote. For short-term (first-year) decomposition, nonlinear regressions of exponential or power function form were obtained with  $r^2$  values of 0.82 and 0.64 for foliar and fine-root litter, respectively, across all biomes included. AUF and AUF:N ratio were the most explanative litter quality variables, while the combined temperature-moisture terms AET (actual evapotranspiration) and CDI (climatic decomposition index) were best for climatic effects. Regressions contained some systematic bias for grasslands and arctic and boreal sites, but not for humid tropical forests or temperate deciduous and coniferous forests. The ability of the regression approach to fit climate-driven decomposition models of the 10-year field results was dramatically reduced from the ability to capture drivers of short-term decomposition. Future work will require conceptual and methodological improvements to investigate processes controlling decadal-scale litter decomposition, including the formation of a relatively stable fraction and its subsequent decomposition.

*Keywords:* climate, decomposition, evapotranspiration, litter quality, mathematical model, stable litter fraction, temperature

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## Introduction

We set out to test the limits of a 30-year-old paradigm in global change science, the interaction of indices of climate and plant litter quality in controlling decomposition rates (Meentemeyer, 1978), with possibly the largest and broadest set of observations yet produced by a single study (Parton *et al.*, 2007; Harmon *et al.*, 2009). The decomposition and partial stabilization of

foliar and fine-root detritus is a key ecosystem process. Rates of decomposition exert strong controls on the amounts and rates of carbon stored in or lost from soils, affecting soil fertility as well as surface-atmosphere exchanges of carbon. Decomposition rates also link to plant community composition both through the types and amounts of litter inputs and through the alteration of soil properties, affecting plant growth through negative or positive feedbacks (Hobbie, 1992; Van Breemen & Finzi, 1998; Berendse, 1999; Whitham *et al.*, 2006).

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Understanding how plant litter decomposition and the accumulation of stable fractions are likely to be altered by species and climate changes is key in simulating or forecasting future carbon cycling. Rates of litter decomposition and accumulation exhibit strong differences among biomes, governed by differences in plant species, decomposer communities, edaphic factors, and temperature and moisture regimes (Aerts, 1997). Researchers in ecosystem science and global change have long sought general, predictive principles to describe the controls on plant litter decomposition across gradients, seasons, and biomes. Predictive indices include continuous indices of substrate quality, including the carbon to nitrogen (C/N) mass ratio and 'lignin' (operationally defined as acid unhydrolyzable fraction or AUF; see 'Materials and methods') of the initial (i.e. freshly produced) litter (Cromack *et al.*, 1975; Berg & Staaf, 1981). The ratio of lignin:N or AUF:N has also been widely explored for decades because it incorporated both potential, bioavailable metabolic energy for decomposer microorganisms and nutrient limitation (Aber & Melillo, 1982; Taylor *et al.*, 1989).

Thirty years ago, Vernon Meentemeyer (1978) proposed a general set of principles and indices that became a key paradigm in ecosystem and global change science: the combination and interaction of climate and litter quality indices in predicting rates of decomposition. As an index of litter quality Meentemeyer (1978) used lignin and as an index of climate he used actual evapotranspiration (AET), which combined temperature and moisture into a single term. The basis for quantifying a rate of decomposition was a change in litter mass over a field incubation period fit to an exponential decay equation. At the time, few or no data were available to test whether decomposition rates over short to long time periods could be characterized by the same form of equation or the same values of decomposition parameters.

In field experiments designed to test the Meentemeyer (1978) principles more broadly, results have often indicated that over periods of 2–3 years and longer in temperate biomes, decomposition occurs in distinguishable phases. Melillo *et al.* (1989) and Aber *et al.* (1990) incubated foliar and root litter from temperate-forest coniferous and deciduous trees for up to 6.4 years, finding the later phase to begin after ca. 3.5 years or when ca. 20% of the initial mass remained. Aber *et al.* (1990) wrote the following:

'A large regional-scale decomposition experiment to test the generality of these results and to develop relationships that include climatic drivers and so hold over large geographic regions should be a high priority.'

In the two decades since, numerous large-scale decomposition studies and analyses have been conducted. Berg *et al.* (1993) analyzed litter quality and climatic controls on short-term decomposition rates in a single species (*Pinus sylvestris*) across 39 sites in climates from the subarctic to subtropical and Mediterranean, the broadest geographic range studied to that time. Trofymow *et al.* (2002) analyzed litter quality and climatic controls on decomposition in a litter-transplant study using much longer (6 year) field incubations of 10 foliar litters and one wood litter conducted by a collaborative group of investigators using standard methods across 18 sites in Canada.

Here, we analyze the controlling effects of climate and litter quality on decomposition in six genera of foliar and three genera of fine-root litters that were incubated in the field for up to 10 years at 27 sites ranging from the arctic to the tropics. This analysis is part of the Long term Intersite Decomposition Experiment Team (LIDET) study, a highly collaborative, centrally designed and conducted experiment initiated in 1990 using common litters and standard methods across all sites and carried out by a single team of investigators for over 15 years (Moorhead *et al.*, 1999; Gholz, 2000; Parton *et al.*, 2007; Harmon *et al.*, 2009). The results from this 10-year field experiment, we believe, represent both the longest-term study and broadest range of litter qualities, climates, and litter-climate combinations yet included in a single study. Previous broad-scale analyses of litter quality and climatic controls on decomposition have either analyzed the results from different investigative teams using a variety of field and laboratory methods, considered shorter time scales, or included less breadth in the ranges of litter quality or climate.

Our objectives in the present analysis were threefold: (i) to evaluate traditional climatic and litter-quality indices (for example AET and 'lignin,' or AUF) as independent, continuous variables correlating with decomposition rates across broad ranges and novel litter × climate combinations; (ii) to evaluate the strengths and limitations of climate and litter-quality indices as correlating with decomposition rates over the short vs. long term (1–10 years); (iii) to explore whether alternative indices of litter quality and climate would provide better independent variables accounting for decomposition rates across broad and novel combinations of litter and climate.

## Materials and methods

### *Study sites, standard litters, and field incubation periods*

The standard set of LIDET litters we consider here included foliage and roots from herbaceous and woody

plants, came from a wide range of native biome types, and covered a wide range in initial litter quality (Table 1). Initial nitrogen (N) concentrations in these litters ranged from 0.36% (*Pinus elliotii* roots) to 1.97% (*Drypetes glauca* leaves), while AUF concentrations ranged from 10.5% (*Schizachyrium gerardi* roots) to 34.9% (*P. elliotii* roots). LIDET study litters spanned a >10-fold range in the ratio of AUF:N (5.53 for *D. glauca* leaves to 59.5 for *P. elliotii* leaves). Mean annual air temperatures among the 27 sites ranged from  $-7$  to  $26$  °C, while mean annual precipitation (MAP) ranged from 24.0 to 410 cm (Table 2). Our sites spanned a sevenfold range in AET (ca. 24–170 cm), or approximately triple the range in AET used by Meentemeyer (1978). An important feature of the LIDET study design was that the wide range in litter quality together with the cross-biome transplants produced numerous novel combinations of litter  $\times$  climate. (Each standard litter was also incubated at its native site; these combinations are included in the present analysis.)

Fresh plant litter was collected in the field, sorted by species, air dried ( $25$  °C) and shipped to Oregon State University where it was placed in mesh litter bags. Leaf litter bags had a top mesh of 1 mm nylon and a bottom of  $55$   $\mu$ m Dacron. Fine root litter bags were entirely of  $55$   $\mu$ m Dacron mesh (Harmon *et al.*, 2009). Each leaf litter bag contained 10 g of air-dried litter from a single species; each fine root litter bag contained 5–7 g of air-dried litter from a single species (fine roots <2 mm diam.). Here, we analyze the results from the set of six standard genera of foliar litter and three standard genera of root litter (Table 1) that were incubated across all participating sites (for one genera of foliar litter, *Pinus*, two species were included but neither had complete coverage across all sites; Table 1). These standard litters were shipped to each participating field site where they were incubated in the field, beginning in fall 1990 or 1991, for 10 years or until too little mass remained to collect (as in some tropical sites after only a few years).

At each site, litter bags were placed together as a group in a location representative of edaphic and microclimatic conditions at the site. Foliar litter bags were placed aboveground at the top of the litter layer in fall 1990; subsequent litterfall was allowed to accumulate atop the bags. Fine root litter bags were buried in upper 20 cm of mineral soil at a  $45^\circ$  angle with one edge at the surface and with the mineral soil pressed firmly down onto the bags (Harmon *et al.*, 2009). Litter bags were collected at each site once per year in the fall (exceptions were tropical sites, Barro Colorado Island, Guanica, La Selva, Luquillo, and Monteverde, where bags were collected every 3–6 months) and shipped to Oregon State University for analysis. Nine standard litters at 27

sites would yield 243 combinations, but a few were removed because of questionable data. We also added a small number of litter  $\times$  site combinations where standard litters were incubated as 'wildcard' litters (which were part of the larger LIDET study otherwise not analyzed here). Overall this produced 251 litter (foliar or root, and species)  $\times$  site combinations. Each litter  $\times$  site combination comprised up to 10 collection dates (once per year for 10 years) with two to four replicates. Each began with four replicates, but some bags were lost to fire, burial, and other disturbances. The present analysis thus includes data from more than 7000 litter bags.

At the start of the study, subsamples of fresh litter were oven dried ( $70$  °C), ground in a Wiley Mill, and used to quantify numerous characteristics of initial litter chemistry (i.e. litter quality) at Oregon State University. Carbon (C) and nitrogen (N) concentrations were determined by dry combustion on a Leco C/N/S-2000 Macro Analyzer (Leco Corporation, St. Joseph, MI, USA). Ash content (Ash) was determined via loss on ignition in a muffle furnace ( $450$  °C for 8 h). Analysis of C 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 (hereafter referred to as the 'water soluble' fraction) 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). AUF content, often commonly referred to as 'lignin' (Meentemeyer, 1978; Aber *et al.*, 1990), was determined by hydrolyzing extractive-free material with sulfuric acid and weighing the insoluble fraction (Effland, 1977; Obst & Kirk, 1988). It is important to note that, in addition to capturing true molecular lignins, this operationally defined acid hydrolysis used to quantify what is commonly referred to as 'lignin' also captures some waxes and other organic residues (Preston *et al.*, 1997). Hydrolysates were analyzed for carbohydrate content using the phenol-sulfuric acid assay (DuBois *et al.*, 1956) and hereafter referred to as 'acid-soluble carbohydrates'.

After collection from the field, foreign material (including ingrown roots) was removed by hand from each litter bag. Litter was dried ( $55$  °C), weighed, and a subset analyzed for Ash as described above for fresh litter. Given the large number of samples in this study, it was not feasible to analyze litter chemistry in every postfield-incubation sample using traditional wet-chemistry methods; instead, wet chemical analyses were performed on a representative subset and

**Table 1** Initial chemical characteristics of the standard LIDET litters used in the present analysis (*n1* = number of samples used for analysis of initial litter chemistry; *n2* = number of litter site combinations in field incubations analyzed here) (Harmon *et al.*, 2009)

Species*	<i>n1</i>	<i>n2</i>	Ash (%)	NPE (% aD)†	WS (% aD)†	AS (% aD)†	AUF (% aD)†	Tannin (% aD)†	WS Carb (% aD)†	AS Carb (% aD)†	Mass ratios			
											C (%)	N (% aD)	C/N	AUF/N
<i>Leaves</i>														
ACSA	5	27	4.7	8.2	48.2	27.6	16.0	7.7	11.1	12.7	49.8	0.81	61.8	19.8
DRGL	8	27	7.8	8.0	40.6	40.3	11.0	8.0	13.3	18.1	47.8	1.97	24.2	5.6
PIEL	5	15	1.5	17.4	19.7	41.5	21.5	4.5	6.8	20.3	54.3	0.36	163.8	59.7
PIRE	5	21	1.7	15.3	20.7	44.7	19.3	7.4	9.8	20.1	53.4	0.59	92.7	32.8
QUPR	8	27	4.4	9.4	27.4	39.6	23.6	6.9	7.1	18.0	51.5	1.03	50.5	23.0
THPL	7	27	7.8	14.6	26.3	37.6	21.5	4.4	9.0	16.5	51.1	0.62	83.1	34.5
TRAE	5	27	2.8	3.4	6.8	73.6	16.3	2.9	5.0	41.1	47.3	0.38	133.3	43.2
<i>Roots</i>														
ANGE	8	27	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	27	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	26	6.3	8.9	19.8	36.1	35.2	3.3	8.5	19.7	49.4	0.82	61.5	43.0

\*ACSA, *Acer saccharum*, sugar maple; ANGE, *Schizachyrium gerardi*, big bluestem; DRGL, *Drypetes glauca*, a tropical broadleaf; PIEL, *Pinus elliotii*, slash pine; PIRE, *Pinus resinosa*, red pine; QUPR, *Quercus prinus*, chestnut oak; THPL, *Thuja plicata*, western red cedar; TRAE, *Triticum aestivum*, wheat.

†NPE, nonpolar extractives; WS, water soluble extractives; AS, acid soluble fraction; AUF, acid unhydrolyzable fraction; Tannin, condensed tannins; WS Carb, water soluble carbohydrates; AS Carb, acid soluble carbohydrates; C, carbon; N, nitrogen; af, ash-free.

**Table 2** List of the field sites where litter was incubated, with biome types, geographic coordinates, and climatic variables used in the analysis (Harmon *et al.*, 2009)

Field site	Code	Geographical coordinates	Elev (m)	Biome type	MAP (cm)	MAT (°C)	AET (cm)	PET (cm)	CDI
H.J. Andrews Exper. Forest, OR, USA	AND	44°14'N	500	Temperate Coniferous Forest	230.9	8.6	76.4	98.2	0.23
Toolik Lake, AK, USA	ARC	63°38'N	760	Arctic Tundra	32.7	-7.0	28.4	42.3	0.08
Barro Colorado Island, Panama	BCI	9°10'N	30	Humid Tropical Seasonal Forest	269.2	25.6	136.8	151.7	0.78
Bonanza Creek Exper. Forest, AK, USA	BNZ	64°45'N	300	Boreal Forest	40.3	-5.0	36.0	57.6	0.10
Blodgett Research Forest, CA, USA	BSF	38°52'N	1300	Temperate Coniferous Forest	124.4	14.4	75.3	109.7	0.16
Cedar Creek Natural History Area, MN, USA	CDR	45°24'N	230	Temperate Savanna	82.3	5.5	73.3	102.6	0.29
Central Plains Exper. Range, CO, USA	CPR	40°49'N	1650	Temperate Shortgrass Steppe	44.0	8.9	43.0	120.2	0.15
Coweeta Hydrological Laboratory, NC, USA	CWT	35°00'N	700	Temperate Deciduous Forest	190.6	12.5	117.3	135.3	0.41
Guánica State Forest, Puerto Rico	GSF	17°57'N	80	Dry Tropical Forest	50.8	26.3	50.2	142.2	0.39
Hubbard Brook Exper. Forest, NH, USA	HBR	43°56'N	300	Temperate Deciduous Forest	139.6	5.0	71.2	81.7	0.28
Harvard Forest, MA, USA	HFR	42°40'N	335	Temperate Deciduous Forest	115.2	7.1	85.1	104.1	0.26
Jornada Exper. Range, NM, USA	JRN	32°30'N	1410	Warm Semi-desert	29.8	14.6	29.2	166.6	0.11
Juneau, AK, USA	JUN	58°00'N	100	Temperate Coniferous Forest	287.8	4.4	49.5	54.4	0.20
Kellogg Biological Station, MI, USA	KBS	42°24'N	288	Temperate Agro Ecosystem	81.1	9.0	70.6	100.7	0.28
Konza Prairie Research Natural Area, KA, USA	KNZ	39°05'N	366	Temperate Tallgrass Prairie	79.1	12.8	74.7	125.0	0.31
La Selva Biological Station, Costa Rica	LBS	10°00'N	0	Humid Tropical Forest	409.9	25.0	169.9	177.3	0.89
Luquillo Experimental Forest, Puerto Rico	LUQ	19°00'N	350	Humid Tropical Forest	336.3	23.0	123.4	125.9	0.84
Loch Vale Watershed, CO, USA	LVW	40°17'N	3160	Boreal Forest	109.6	1.6	85.1	108.3	0.15
Monte Verde, Costa Rica	MTV	10°18'N	1550	Tropical Elfin Cloud Forest	268.5	17.7	108.4	116.6	0.60
North Inlet (Hobcaw Barony), SC, USA	NIN	33°30'N	2	Temperate Wetland	149.1	18.1	120.6	145.6	0.53
North Temperate Lakes, WI, USA*	NILK	46°00'N	500	Temperate Deciduous Forest	67.7	4.4	64.9	88.4	0.21
Niwot Ridge, CO, USA	NWT	40°03'N	3650	Alpine Tundra	124.9	-3.7	64.7	75.6	0.10
Olympic National Park, WA, USA	OLY	47°50'N	150	Temperate Coniferous Forest	153.1	10.0	79.4	104.4	0.23
Sevilleta National Wildlife Refuge, NM, USA	SEV	34°29'N	1572	Warm Semi-desert	25.4	16.0	25.2	160.2	0.09
Santa Margarita Ecological Reserve, CA, USA	SMR	33°30'N	500	Annual Grassland	24.0	16.4	23.6	186.0	0.08
University of Florida, FL, USA	UFL	29°30'N	35	Temperate Coniferous Forest	123.8	21.0	116.6	162.1	0.54
Virginia Coast Reserve, VA, USA	VCR	37°30'N	0	Temperate Wetland	113.8	15.0	99.3	121.5	0.43

AET, actual evapotranspiration; PET, potential evapotranspiration; MAP, mean annual precipitation; MAT, mean annual temperature; CDI, Climate Decomposition Index (unitless).

\*Litter was incubated at NILK for only 3 years; results are used here to analyze short-term but not long-term decomposition.

calibrated to near infrared reflectance spectroscopy (NIRS) measurements (Wessman *et al.*, 1988; McLellan *et al.*, 1991a,b), which were used to analyze the chemistry of the majority of samples (further details are provided by Harmon *et al.*, 2009).

#### Calculation of first-order decomposition constants

We calculated the proportion of initial ash-free dry mass remaining for each individual litter bag at each time of collection. We averaged proportions of mass remaining across replicate litter bags within each standard litter, site, and collection date and normalized each to the percentage of initial mass remaining. This produced 251 time series (for 251 litter  $\times$  site combinations) in percentage of ash-free initial litter mass remaining. Next, to assess the controls on short vs. long-term decomposition rates, we fitted three different mathematical models of first-order (exponential) decomposition to each time series, using the same sets of observational data to fit all three of the mathematical models, described below. We refer to the first-order constants thus determined for the three models as the  $k_S$  (short-term),  $k_4$  (a decadal-scale single-exponential model with a stable asymptote) and  $k_I$  (integrated) constants, described below. We emphasize that these three mathematical models are separate and independent models of the time course of mass loss; they are not additive.

#### Short-term decomposition governed by $k_S$

Our  $k_S$  constant, used only for the first year of incubation, is comparable to the model used by numerous other investigators reporting single-year or first-year results (Meentemeyer, 1978; Berg *et al.*, 1993; Aerts, 1997). In determining  $k_S$  for each litter  $\times$  site combination, we fit the exponential model given by

$$M(t) = M_0 e^{-k_S t} \quad (1)$$

where  $M(t)$  is percentage of initial litter mass remaining at time  $t$  given in years,  $M_0$  is initial litter mass or 100%, and  $k_S$  is in  $\text{yr}^{-1}$ . In all cases for this model we used exactly two points,  $M_0$ , which we constrained to be exactly 100%, and the point nearest to the 1-year collection interval (which ranged from 0.88 to 1.43 years, but averaged 1.01 years across all litter  $\times$  site combinations). We used this actual collection interval and solved Eqn (1) for  $k_S$ , thus fitting the curve exactly through both the initial and 1-year points. Because only two points were fit, the goodness-of-fit of this model is given by  $r^2 = 1.00$ .

#### Decadal-term decomposition governed by $k_4$ and $S_{04}$

For analysis of long-term decomposition given by an exponential model fit to the 10-year time series data we used 'Model 4' from Harmon *et al.* (2009), whose notation we adopt here. This is a single-exponential model with a stable fraction or asymptote. The  $k_4$  constant characterizes the full length of early-phase decomposition, whether it lasts 1 year or 10 years for particular combinations of litter and climate. In determining  $k_4$  for each litter  $\times$  site combination, we fit Eqn (2) to time-series observations in all litter collection points over the entire 10-year study.

$$M(t) = M_{04} e^{-k_4 t} + S_{04}, \quad (2)$$

where  $M(t)$  is the percentage of initial mass remaining at time ( $t$ ) and  $k_4$  is in  $\text{yr}^{-1}$ . The additional parameter  $S_{04}$  has percentage units and is an asymptote representing a stable fraction (Berg *et al.*, 1984; Harmon *et al.*, 2009). Equation (2) was fit to our time-series data using nonlinear regression by determining the model parameters that minimized the sum of squared deviations between the model and the field data (SAS software; SAS Institute 1999). Curves were constrained to pass through the intercept  $M(0)$  between 95% and 100% of initial litter mass; in fact, however, curves all passed through  $M(0) = 100\%$  because the  $S_{04}$  parameter adjusted itself to bring this about. As a measure of goodness-of-fit to the raw data, the  $k_4$  model had an average  $r^2 = 0.76$ .

#### Long-term integrated decomposition governed by $k_I$

As an alternative window into the long-term decomposition rates that occurred across our study, we next considered the 'long-term integrated  $k$  model' developed by Harmon *et al.* (2009), whose notation we adopt here. The  $k_I$  constant quantifies the overall rate of decomposition over the decadal time scale, integrated and weighted over all decomposition stages in a single  $k$  constant, the closest philosophically to Olson's (1963) initial conceptualization of  $k$ . Two steps were used to calculate  $k_I$  (Harmon *et al.*, 2009). First, we estimated the mass remaining at time intervals of 0.1 years predicted by a two-stage or double-exponential model, 'Model 5' developed by Harmon *et al.* (2009), for each litter  $\times$  site combination:

$$M(t) = M_{f05} e^{-k_{f5} t} + M_{s05} e^{-k_{s5} t}, \quad (3)$$

where  $M(t)$  is the percent ash-free mass remaining,  $M_{f05}$  is the initial ash-free mass of fast-decomposing material,  $k_{f5}$  is the decomposition-rate-constant of this fast material,  $M_{s05}$  is the initial ash-free mass of slow-decomposing material,  $k_{s5}$  is the decomposition rate-constant of this slow material, and  $t$  is time in years. Equation (3) was fit to our time-series data using nonlinear regres-

sion by determining the model parameters that minimized the sum of squared deviations between the model and the field data (SAS software; SAS Institute 1999). The sum ( $M_{t05} + M_{s05}$ ) was constrained to be 100% of initial litter mass and the average goodness-of-fit was  $r^2 = 0.85$ .

In the second step in calculating  $k_I$ , predicted percentages of initial litter masses remaining  $M(t)$  are summed over a long period of years, giving  $M_{SS}$ , the accumulation of litter that would occur in the litter layer of an ecosystem under steady-state conditions (i.e., steady-state litterfall fluxes and unchanging decomposition rates). The time integrated average decomposition rate  $k_I$  is then calculated using the method of Olson (1963):

$$k_I = 100/M_{SS}. \quad (4)$$

We checked the model for various accumulation times and used 200 years, a time at which  $k_I$  became virtually time invariant for all site  $\times$  litter combinations in the LIDET study (Harmon *et al.*, 2009). Note that since Eqn (4) is not regression-based, there is no measure of goodness-of-fit.

#### Climate indices

We tested several climatic indices, including AET, mean annual temperature (MAT), MAP, potential evapotranspiration (PET), and the Climate Decomposition Index (CDI). We calculated the values of all climatic indices from actual values over the study period at weather stations in the vicinity of each site (Table 2).

The CDI is a unitless index ranging from 0 to 1, combining the interactive effects of temperature and moisture in a manner meant to predict the broad-scale effects of climate on decomposition rates, with higher values indicating faster rates of decomposition (Parton *et al.*, 2007; Adair *et al.*, 2008). The CDI (formerly known as DEFAC as in Moorhead *et al.*, 1999; Gholz *et al.*, 2000) is used in the Century model of ecosystem biogeochemistry (Parton *et al.*, 1994) to control the turnover rate of litter biomass and soil organic matter pools. Several approaches to calculate CDI were developed during the time period that LIDET data were being analyzed and were tested by Adair *et al.* (2008) using LIDET data. The present analysis makes use of a formulation of CDI that tended to capture differences in decomposition rates well in the LIDET dataset. Values of  $CDI_i$  are calculated monthly as a function of mean monthly air temperature of the  $i$ th month ( $T_i$ ), monthly precipitation ( $PPT_i$ ), and the monthly potential evapotranspiration rate ( $PET_i$ ) using the following equations:

$$CDI_i = F_t(T_i) \times F_w(PPT_i, PET_i), \quad (5)$$

$$F_t(T_i) = 0.56 + 0.45 \arctan(0.097(T_i - 15.4)), \quad (6)$$

$$F_w(PPT_i, PET_i) = \frac{1}{1 + 30 \exp\left(-8.5 \frac{PPT_i}{PET_i}\right)}, \quad (7)$$

where  $F_t(T_i)$  is a temperature effect on decomposition derived by Del Grosso *et al.* (2005). The effect of moisture on decomposition is given by  $F_w(PPT_i, PET_i)$ . We calculated monthly  $PET_i$  (Allen *et al.*, 1998) using solar radiation (calculated from latitude and time of year), monthly average daily minimum and maximum air temperature, and relative humidity. The mean annual value of CDI for each of the sites was calculated by averaging the monthly calculated values of  $CDI_i$ . Here, the mean annual values of CDI ranged 10-fold among sites, from 0.08 to 0.89.

#### Analysis of climate and litter quality controls on decomposition rates

The decomposition constants ( $k_S$ ,  $k_A$ , and  $k_I$ ) were used as dependent variables in statistical analyses to assess the degree to which climate and litter quality measures (as independent variables) could account for decomposition rates over different time scales. Because predicting decomposition using Model 4 [Harmon *et al.*, 2009, Eqn (2)] also requires prediction of the stable asymptote  $S_{04}$ , we analyzed  $S_{04}$  as an additional dependent variable. We performed two types of least-squares regression of the four dependent variables against climate and litter quality measures (working in the STATA SE 10.0 software for statistical analysis, StataCorp LP, College Station, TX, USA). First we used linear regressions (Moore *et al.*, 1999; Preston *et al.*, 2000; Trofymow *et al.*, 2002; Liski *et al.*, 2003). We performed stepwise multiple linear regressions (Trofymow *et al.*, 2002), in which the most highly significant independent variable (if  $P < 0.05$ ) entered the regression model first and additional variables entered stepwise, but only if significant ( $P < 0.05$ ). We tested climatic indices alone, litter quality indices alone, and climate-litter quality terms in combination for foliar and root data combined, foliar data alone, and roots alone (251, 171, and 80 litter  $\times$  site combinations, respectively). As independent variables we included all of the variables listed in Tables 1 and 2, as well as terms that combined individual variables. Combined terms included the ratio of AUF:N (often referred to as 'lignin':N), the ratio of C/N, the 'lignocellulose index' (LCI; Aber *et al.*, 1990; Preston *et al.*, 2000), defined as  $AUF/[AUF + \text{acid-soluble (AS) fraction}]$ , and total extractives (nonpolar (NPE) + water-soluble (WS) extractives) (Aber *et al.*, 1990; Currie & Aber, 1997).

Next, we used nonlinear regressions with the same sets and combinations of dependent and independent variables to assess possible nonlinear relationships. Specifically, in preliminary analyses we found that using  $\ln(k)$  as an independent variable in linear regressions produced better regression models than untransformed values of  $k$ . We note that a linear regression for  $\ln(k)$ :

$$\ln(k) = ax_1 + bx_2 + c \quad (8)$$

is equivalent to a nonlinear regression for  $k$ :

$$k = \exp(ax_1 + bx_2 + c) = e^{ax_1} e^{bx_2} e^c \quad (9)$$

where  $a$ ,  $b$ , and  $c$  are parameters fit through nonlinear least-squares regression and the  $x_i$  are independent variables representing climate and litter quality. We generalized this to the nonlinear equation:

$$k = a \exp(bx_1 + cx_2 + \dots + d) \quad (10)$$

which we tested and found to supply the best nonlinear regression in many cases.

Another form of nonlinear equation that we found to be highly useful was a power function form. Aerts (1997) and Preston *et al.* (2000) used equations of the following form to fit first-order decomposition constants  $k$ :

$$k = ax^b \quad (11)$$

where  $a$  and  $b$  are parameters fit through nonlinear least-squares regression and ( $x$ ) was either a single independent variable or a ratio of variables (e.g., AUF:N). We generalized this functional form to:

$$k = ax_1^b x_2^c x_3^d \dots + g \quad (12)$$

where  $x_1$ ,  $x_2$ , and  $x_3$  are independent variables (or ratios of variables) and  $a$ ,  $b$ ,  $c$ ,  $d$  and  $g$  are parameters fit as real numbers through nonlinear least-squares regression.

We assessed the quality of fit of each regression model for each  $k$  constant. Because  $r^2$  values reported by statistical software for nonlinear regressions did not accurately represent the relationship between predicted and observed values of the dependent variable, we generated predicted values of  $k$  using the best regressions we found and then separately calculated the goodness of fit between the observed and predicted values of  $k$  (Liski *et al.*, 2003). This was estimated as the value of  $r^2$  obtained by fitting Eqn (13), a linear regression with a constant included:

$$k_{\text{pred}} = ak_{\text{obs}} + b, \quad (13)$$

where  $k_{\text{pred}}$  and  $k_{\text{obs}}$  are the predicted and observed values of  $k$ , respectively.

In addition to the linear and nonlinear regressions, we analyzed the effects of climate and litter quality variables on decomposition model parameters  $k_S$ ,  $k_4$ ,  $S_{04}$ , and  $k_1$  using analysis of variance (ANOVA). We

performed two-way ANOVAs analyzing climate and litter quality effects on each decomposition model parameter across all foliar and root litter combined across all litter  $\times$  site combinations. In each ANOVA we tested a single climate variable (or site as a categorical variable), a single litter quality variable (that which had the highest statistical significance in stepwise linear regressions against  $k_S$ ,  $k_4$ ,  $S_{04}$ , and  $k_1$  individually) and the interaction of the climate  $\times$  litter quality variable.

Raw time-series data for the study can be found on the H.J. Andrews LTER website: <http://www.fsl.orst.edu/lter/research/intersite/lidet.htm>. Details for the decomposition model fits to the raw data can be found at the archival Knowledge Network for BioComplexity website: <http://knb.ecoinformatics.org/index.jsp>

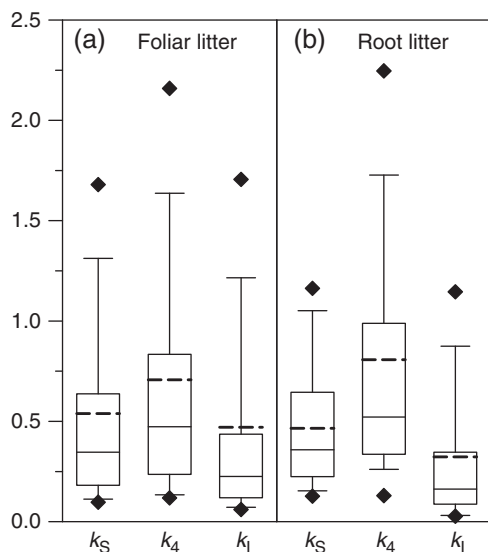
## Results

### *Parameter values in decomposition models*

Across all litter and sites, values of the short-term (first year) decomposition constant  $k_S$  ranged from 0.035 to 3.5 year<sup>-1</sup> with an overall mean of 0.52 year<sup>-1</sup>. The distribution was highly skewed toward low values, with a median of 0.35 year<sup>-1</sup> and 95th percentile of 1.5 year<sup>-1</sup>. Distributions of  $k_S$  were similar when separated into foliar and fine root litter (Fig. 1), although values were slightly higher for foliar vs. fine root litters (mean  $k_S$  = 0.54 year<sup>-1</sup>, 0.47 year<sup>-1</sup>, respectively).

Our two long-term models were Model 4 (Harmon *et al.*, 2009) governed by the decomposition constant  $k_4$  and stable asymptote  $S_{04}$  and the long-term integrated model governed wholly by the first-order decomposition constant  $k_1$ . In Model 4, values of  $k_4$  for foliar and root litters had means higher than those of the short-term constant  $k_S$  (Fig. 1). These were offset by the presence of the stable asymptote  $S_{04}$ , which reduced the overall mass loss. Values of  $S_{04}$  averaged 24.7% of initial litter mass. Values of the stable asymptote had a high range, from zero, which occurred in 39 site  $\times$  litter combinations across a wide range of litters and biomes, to 73.3%. Nine of the highest 11 values of  $S_{04}$  occurred in the same species (*P. elliotii*, both needles and roots) incubated across sites that ranged widely in annual AET, from 28.4 cm in arctic tundra (ARC) to 108.4 cm in tropical cloud forest (MTV). Thus, at least in the extreme values for the long-term stable fraction of litter, species exerted a stronger control than climate. Interestingly, averaged over all sites in the study, fine root litter had a higher stable fraction (mean  $S_{04}$  = 32.7%) as well as a higher value of  $k_4$  (mean 0.81 year<sup>-1</sup>) compared with foliage (mean  $S_{04}$  = 20.9%, mean  $k_4$  = 0.71 year<sup>-1</sup>).





**Fig. 1** Box plots of values of  $k$  ( $\text{year}^{-1}$ ) for the three decomposition models. Boxes show 25th percentile, median, and 75th percentile values; whiskers show 10th and 90th percentiles, diamonds show 5th and 95th percentile values. Dashed lines indicate mean values. (a) Foliar litter across all sites; (b) fine root litter across sites.

For the majority of litter  $\times$  site combinations, decomposition rates slowed after the first year more than would be predicted by a single-exponential model fit to first-year results. Average values of the  $k_1$  for the long-term integrated model were lower than those for both the  $k_S$  and  $k_4$  models. Values of  $k_1$  had a mean of  $0.42 \text{ year}^{-1}$  and median of  $0.21 \text{ year}^{-1}$ , with a distribution even more highly skewed toward low values than the  $k_S$  model (Fig. 1). It should be noted that the values and ranges of all of our decomposition constants are dependent on the litter types and litter-climate combinations tested.

#### *Climate and litter quality control on decomposition model parameters*

In the manner of Meentemeyer's (1978) synthesis diagram, we graphed our results for both the  $k_S$  and  $k_1$  constants against the AUF for 10 selected sites representing the range of biomes in our study (Fig. 2). If the biomes are separated into very broad categories of AET such as very low (including boreal forest and arctic tundra), intermediate (including dry tropical forests and temperate forests), and very high (including humid tropical forest), Meentemeyer's (1978) suggested patterns of higher values of  $k$  at higher AET and greater slope in the relationship between  $k$  and AUF with increasing AET did hold. When values of AET were closer together, however, as in individual site by site

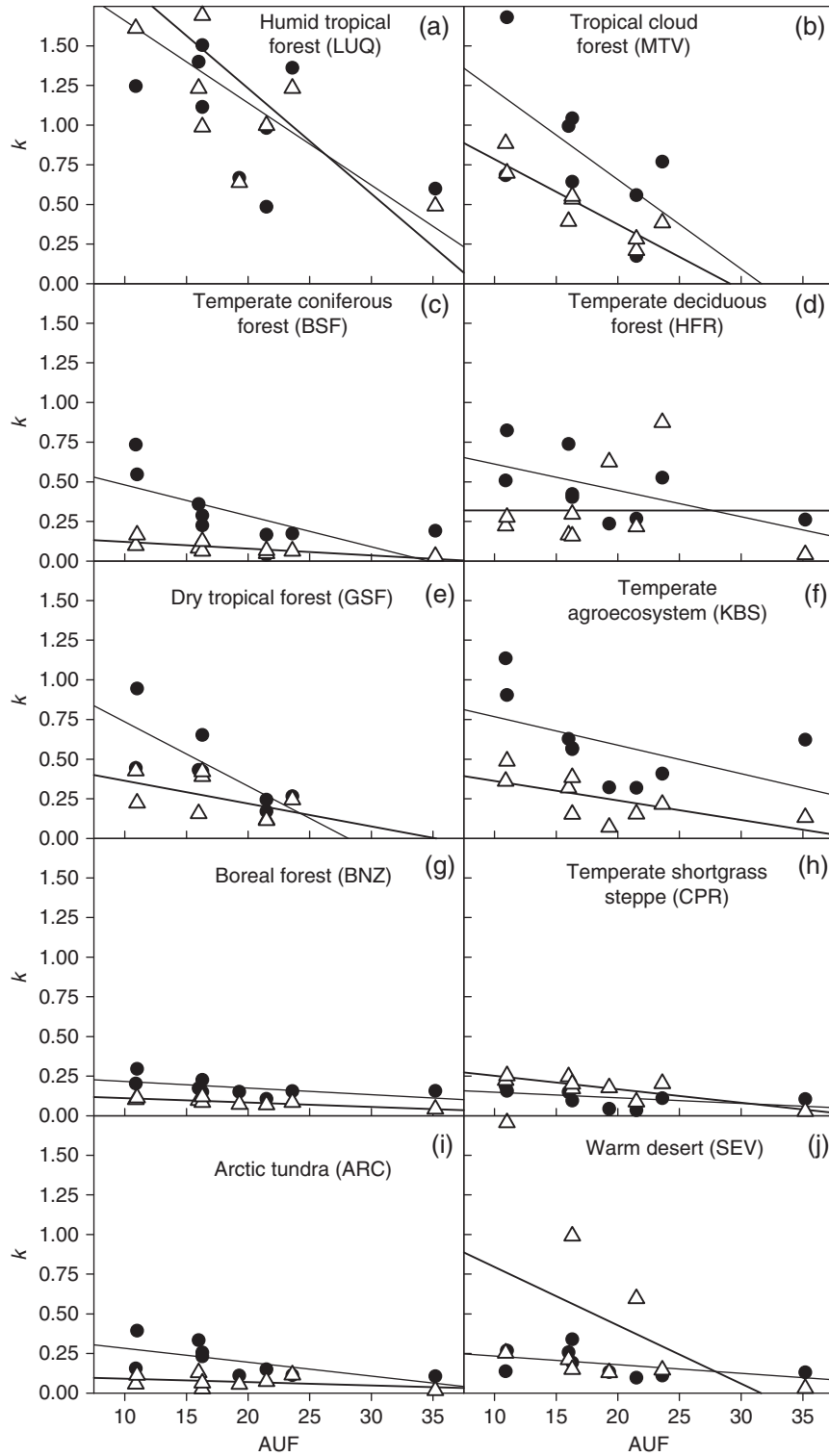
comparisons, the values of  $k$  constants did not follow such a reliable pattern.

The Meentemeyer-style graphical analysis (Fig. 2) shows our result that most values of the decadal-scale  $k_1$  constants were lower than the short-term  $k_S$  values, but also shows that exceptions to that generalization tended to occur at particular sites. The warm desert site SEV exhibited three  $k_1$  values that were much higher than the regression line for  $k_S$  values for the site (Fig. 2j). At the temperate shortgrass steppe site CPR, eight of the nine litters had values of  $k_1$  greater than those of  $k_S$ , indicating that decomposition rate, as a proportion of remaining mass, accelerated after the first year. But these sites were in the minority. When decomposition constants were summarized by site, only seven of the 27 field sites had mean values of  $k_1$  greater than those of  $k_S$  (CPR, JUN, LUQ, NIN, NLK, SEV, and VCR).

Climate indices alone were better predictors of decomposition rates than litter quality variables alone, as revealed by stepwise linear regressions of  $k$  constants against all climatic and litter quality variables in our study. However, litter quality indices did contribute to predictability. The best single litter-quality predictor of decomposition rates was the AUF:N ratio. When included in linear regressions, the AUF:N ratio uniformly improved the goodness-of-fit of regressions over each climatic index considered alone (Table 3).

Among AET, MAP, MAT, and PET, AET was the superior climatic index correlating with  $k$  constants of all three mathematical models of decomposition across all litter  $\times$  site combinations (Table 3). The climatic decomposition index (CDI) formulated using an *arctan* function of monthly temperatures, as previously tested using LIDET data (Adair *et al.*, 2008) and chosen for analysis here, improved the  $r^2$  of linear regressions for all  $k$  constants over those using AET, both with and without the inclusion of litter quality (Table 3). Strong climatic effects on  $k_S$  were also evident when litters were analyzed individually across the full range of sites. Correlations of  $k_S$  with CDI were significant for each litter individually with  $r^2$  values ranging from 0.53 (*S. gerardi* roots) to 0.87 (*T. aestivum* foliage; data not shown). The same was true for AET, although  $r^2$  values were somewhat lower; correlations with  $k_S$  for individual litters ranged from 0.41 (*D. glauca* roots) to 0.73 (*Q. prinus* foliage).

To explore potentially new combinations of predictive variables on decomposition parameters, we tested nonlinear regressions using all of the independent variables in this study and in various forms of nonlinear equations (see 'Materials and methods'). We found that for the short-term decomposition constant  $k_S$  it was possible to capture up to 82% of the variance in decom-



**Fig. 2** Values of decomposition constants  $k_5$  (solid circles) and  $k_1$  (open triangles), in  $\text{year}^{-1}$ , plotted against acid unhydrolyzable fraction (AUF) of initial litter. Each panel includes results from a single field site, together representing the partial range of sites in the LIDET study (Table 2). Panels are ordered, top to bottom, with decreasing values of AET and CDI (Table 2). Site-specific linear regression lines for each  $k$  constant against AUF are shown. (Two high data values are not shown:  $k_5 = 2.49 \text{ year}^{-1}$  and  $k_1 = 2.87 \text{ year}^{-1}$  at site LUQ.)

**Table 3** Goodness-of-fit ( $r^2$  values) and significance<sup>1</sup> of linear regressions of climate variables<sup>‡</sup> and AUF:N (ratio of acid insoluble fraction nitrogen) to predict parameters  $k_S$ ,  $k_4$ ,  $S_{04}$ , and  $k_I$  of decomposition models

Parameter	Climatic index alone					Climatic index together with AUF:N ratio				
	MAP	MAT	AET	PET	CDI	MAP	MAT	AET	PET	CDI
$k_S$	0.29 <sup>†</sup>	0.25 <sup>†</sup>	0.38 <sup>†</sup>	0.12 <sup>†</sup>	0.46 <sup>†</sup>	0.44 <sup>†</sup>	0.40 <sup>†</sup>	0.53 <sup>†</sup>	0.26 <sup>†</sup>	0.61 <sup>†</sup>
$k_4$	0.17 <sup>†</sup>	0.16 <sup>†</sup>	0.26 <sup>†</sup>	0.06***	0.30 <sup>†</sup>	0.25 <sup>†</sup>	0.23 <sup>†</sup>	0.34 <sup>†</sup>	0.13 <sup>†</sup>	0.38 <sup>†</sup>
$S_{04}$	0.06***	0.09 <sup>†</sup>	0.06***	0.04**	0.11 <sup>†</sup>	0.07***	0.10 <sup>†</sup>	0.07***	0.05**	0.13 <sup>†</sup>
$k_I$	0.09 <sup>†</sup>	0.08 <sup>†</sup>	0.11 <sup>†</sup>	0.02*	0.16 <sup>†</sup>	0.10 <sup>†</sup>	0.09 <sup>†</sup>	0.12 <sup>†</sup>	0.03*	0.17 <sup>†</sup>

<sup>1</sup>Significance: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , <sup>†</sup> $P < 0.0001$ .

<sup>‡</sup>Climatic variables are as in Table 2.

Regressions were performed over all foliar and root litter combined and across all litter × site combinations.

AET, actual evapotranspiration; PET, potential evapotranspiration; MAP, mean annual precipitation; MAT, mean annual temperature; CDI, Climate Decomposition Index (unitless).

**Table 4** Regression models to predict first-order decomposition constants  $k_S$ ,  $k_4$ , and  $k_I$ , together with the decadal-scale stable fraction  $S_{04}$  from climate and litter quality variables across all sites

Foliar litter	$r^2$	Fine root litter	$r^2$
<i>(a) Best regression equations using all variables</i>			
$k_S = CDI^{1.06} NPE^{-0.839} WSCarb^{0.703} ASh^{0.512}$	0.82***	$k_S = 0.476 \exp(1.54CDI - 0.0319AUF)$	0.64***
$k_4 = 51.5CDI^{1.38} \left(\frac{AUF}{N}\right)^{-0.524} npe^{-0.753} + 0.194$	0.66*	$k_4 = CDI^{0.575} N^{-1.61}$	0.25***
$S_{04} = CDI^{-0.489} \left(\frac{AUF}{N}\right)^{0.321} WS^{0.400}$	0.17***	$S_{04} = CDI^{-0.309} AUF^{0.658} AS^{0.278}$	0.28**
$k_I = 0.0888 \exp(2.12CDI - 0.0241\left(\frac{AUF}{N}\right) + 0.0314AS)$	0.25**	$k_I = \exp\left(2.22CDI - 2.84\left(\frac{AUF}{AUF+AS}\right) - 1.28\right)$	0.27*
<i>(b) Best regression equations using all climate variables but only AUF and N for litter quality</i>			
$k_S = 33.4CDI^{1.05} AUF^{-1.04} N^{0.241}$	0.78*	$k_S = 0.476 \exp(1.54CDI - 0.0319AUF)$	0.64***
$k_4 = 11.5CDI^{1.44} \left(\frac{AUF}{N}\right)^{-0.566} + 0.223$	0.57*	$k_4 = CDI^{0.575} N^{-1.61}$	0.25***
$S_{04} = 36.4 \exp(-2.02CDI)$	0.13***	$S_{04} = CDI^{-0.343} \left(\frac{AUF}{N}\right)^{0.890}$	0.27***
$k_I = 0.614 \exp(2.09CDI - 0.0614AUF)$	0.21*	$k_I = \exp(1.99CDI - 0.0851\left(\frac{AUF}{N}\right))$	0.25***

Regression equations are given separately for foliar litter and fine root litter. Best regression equations are shown using (a) all climate and litter quality variables; (b) all climate variables and only AUF and N for litter quality. Following  $r^2$  values are the significance of the least significant term entering each regression:

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

Climate and litter quality variables are as in Tables 1 and 2.

position of foliar litter and 64% of the variance in decomposition of root litter [Table 4(a)]. CDI was a superior climatic index over AET and other climatic variables in each equation obtained. AUF:N was the single most common litter quality variable to appear in the best equations, although other litter quality variables were significant for some parameters. These included the AS fraction, NPE, WS extractives, water-soluble carbohydrates (WSCarb), and Ash.

*Reduced predictability of long-term decomposition parameters*

As with the short-term decomposition constant  $k_S$ , the long-term (decadal scale) decomposition constants  $k_4$

and  $k_I$  were best modeled with regressions that were nonlinear and included variables representing both climate and litter quality. However, a substantial drop in predictive capacity occurred at the decadal time frame. This was evident in both the linear (Table 3) and nonlinear (Table 4) regressions for  $k_4$  and  $k_I$  constants. Nonlinear regression to predict  $k_4$  for foliar litter exhibited a substantially higher value of  $r^2$  than that for  $k_I$  [ $r^2 = 0.66$  vs.  $0.25$ , respectively; Table 4(a)]. However, the predictability of  $S_{04}$  was much lower [Table 4(a)]. We thus found, for foliage, a relatively good mathematical prediction of the rate of approach to the stable fraction but a poor ability to predict the proportion of the stable fraction. To predict litter mass remaining at any point in time, Model 4 requires both  $k_4$  and  $S_{04}$ .

*Interaction of climatic and litter quality controls*

While climate and litter quality both exerted significant control over litter decomposition parameters, their interaction exerted varying degrees of control. Analysis of variance (Table 5) shed light on several key aspects of this interaction. For our decadal-scale integrated model governed wholly by  $k_I$  with no stable asymptote, the climate-litter quality interaction effect was more significant than each direct effect. Somewhat similarly, for our short-term decomposition model governed wholly by  $k_S$ , the interaction effects of litter quality and climate were significant, in fact more significant than litter quality as a direct effect in most cases (Table 5). One difference between the long-term  $k_I$  parameter and short-term  $k_S$  parameter was that climatic variables did exert a highly significant direct effect over the short term (Table 5). More noticeable, however, was that the model containing a stable asymptote contrasted strongly with both models ( $k_S$  and  $k_I$ ) that lacked one: in Model 4, a climate-litter quality interaction effect was not significant. Thus, climate-litter quality interactions in ANOVA models offered explanatory power only when a stable fraction was omitted from the models.

A second key and interesting feature of our ANOVA results concerned the importance of field site as a categorical factor. Field site showed a significant direct effect, a significant interaction effect with litter quality, and produced a better overall model  $r^2$  than did climate variables (Table 5). This indicates that decomposition model parameters were controlled by site-specific effects across field sites and biomes but that those effects were not fully captured by MATs, precipitation, evapotranspiration or CDI.

**Discussion***Extension of the climatic range to predict short-term decomposition*

Through the efforts of dozens of individuals over more than a decade, the LIDET study (Moorhead *et al.*, 1999; Gholz *et al.*, 2000; Parton *et al.*, 2007; Adair *et al.*, 2008; Harmon *et al.*, 2009) examined litter decomposition over a climatic range that extended beyond that previously used in a single coordinated study. It also used novel and extreme combinations of climate and litter quality

**Table 5** Significance<sup>1</sup> of model terms in two-way ANOVA analyzing climate and litter quality effects on decomposition model parameters  $k_S$ ,  $k_4$ ,  $S_{04}$ , and  $k_I$

	Site	MAP	MAT	AET	CDI
$k_S$					
Site or climate variable	†	†	†	†	†
Litter quality: AUF:N ratio	†	ns	*	ns	ns
Interaction of climate and litter quality	**	†	**	†	†
Model $r^2$	0.75	0.47	0.42	0.56	0.66
$k_4$					
Site or climate variable	†	†	†	†	†
Litter quality: AUF:N ratio	†	ns	ns	ns	ns
Interaction of climate and litter quality	ns	ns	ns	ns	**
Model $r^2$	0.59	0.26	0.24	0.35	0.40
$S_{04}$					
Site or climate variable	*	**	**	*	**
Litter quality: condensed tannins	*	*	*	ns	ns
Interaction of climate and litter quality	ns	ns	ns	ns	ns
Model $r^2$	0.44	0.08	0.11	0.08	0.13
$k_I$					
Site or climate variable	ns	ns	ns	ns	ns
Litter quality: acid soluble carbohydrates	*	ns	ns	ns	ns
Interaction of climate and litter quality	*	*	*	**	**
Model $r^2$	0.48	0.12	0.11	0.15	0.21

<sup>1</sup>Significance: ns, not significant.

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , † $P < 0.0001$ .

‡Climate variables are as in Table 2; Litter quality variables are as in Table 1.

Each of the 20 ANOVA analyses shown here tested a single climate variable<sup>‡</sup> (or site as a categorical variable), the most statistically significant single litter quality variable for each decomposition parameter as shown, and the interaction of the climate \*litter quality variable. Each ANOVA was performed across all foliar and root litter combined and all litter × site combinations.

that do not occur naturally and that had not been previously examined in field studies. A key finding here regards extension of the climate-litter quality paradigm, in which continuous variables are used in regressions to derive first-order  $k$  constants for decomposition models. For short-term (first-year) decomposition rates, and judging by overall model  $r^2$  values, this paradigm did extend over this broad (sevenfold range in AET) and novel range of climates and biome-litter transplants (but see caveats below about biases for certain biomes).

It was no surprise that AUF and AUF:N were the most highly predictive litter quality variables, both because the LIDET litters spanned a wide range (> 10-fold) in AUF:N ratios and because many past studies have found this ratio to correlate with decomposition rates (Aerts, 1997; Preston *et al.*, 2000; Trofymow *et al.*, 2002). Some previous investigators suggested that the LCI should control long-term decomposition constants (Berg *et al.*, 1984; Melillo *et al.*, 1989; Aber *et al.*, 1990), but our tests using both linear and nonlinear regressions found AUF alone or the AUF:N ratio to be superior. In one case, the  $k_1$  model for fine root litter, the LCI was found to be the best litter quality variable [Table 4(a)].

The best forms of nonlinear regression equations we obtained were power function forms in most cases and generalized exponential forms in the others [Table 4(a)]. We suggest that there are several reasons why these were superior to linear regressions. First, these functions allow a curvilinear relationship between the dependent variable and each independent variable. The skewed distributions of  $k$ -values we obtained (Fig. 1) suggest that a ln-transformation of  $k$  values is appropriate. In addition, both nonlinear forms allow for a multiplicative relationship, as opposed to an additive relationship, among litter quality and climatic variables. In analysis of several species of native *Pinus* litter incubated in 39 pine forest sites across a broad range in climate, Berg *et al.* (1993) did not find curvilinear relationships between mass loss and independent climate and litter-quality variables. As a result, Berg *et al.* (1993) emphasized the use of linear regressions of independent variables to account for rates of first-year mass loss. In contrast, in a previous analysis of 5-year LIDET results, Gholz *et al.* (2000) did identify curvilinear relationships between first-order  $k$  constants and climatic indices. In the LIDET study, the broader ranges both in litter types and incubation biomes introduced greater complexity in the combinations of litters and ecosystems relative to that considered by Berg *et al.* (1993). Similarly, in the CIDET study, Trofymow *et al.* (2002) employed linear regressions of independent variables to explain  $\ln(\% \text{ mass remaining})$ , which equates to our nonlinear regression for  $k$  constants using an ex-

ponential equation. This includes both curvilinear relationships between the independent and dependent variables and multiplicative relationships among independent variables.

#### *Temperature, moisture, and their combination*

Literature has been divided on whether temperature and moisture are more predictive of decomposition constants as direct effects or in combined temperature-moisture terms such as AET and CDI. In a study of tropical broadleaf litter in Hawai'i, along an aspect-controlled gradient in moisture where temperatures did not vary, Austin & Vitousek (2000) found differences in MAP alone to account for differences of up to 70% of litter mass remaining in 2-year incubations. In the Canadian Intersite Decomposition Experiment (CIDET) study, a regional study across Canada that involved litter transplants similar to our own (including 10 foliar litters incubated across 19 sites), Trofymow *et al.* (2002) found that MAT, summer precipitation, and winter precipitation were significant and highly explanative of variability in mass losses, although combined temperature-moisture terms were not tested. In contrast, Berg *et al.* (1993) found that AET was the dominant variable controlling litter decomposition rates in pine forests over an AET range 33.0–92.0 cm that spanned the geographic area of nearly all of Europe plus selected North American sites. In an analysis of first-year mass loss across 44 litters from separate studies conducted in temperate, Mediterranean, and tropical regions, Aerts (1997) found AET to be the best overall predictor of variability in first-order  $k$  constants.

In the present study, we tested the direct measures MAT and MAP alongside the combined temperature-moisture terms AET and CDI in several ways: stepwise linear regressions, nonlinear regressions, and analyses of variance. We found AET and CDI to be superior predictors of LIDET decay constants over both short (1 year) and long (10 year) time scales. AET has since filled this role for decades, partly because of its widespread availability as climate data. But investigators have sought to formulate and test improved functions to represent temperature and moisture effects that continue to be based on widely available temperature and moisture data. This includes the CDI used here (Adair *et al.*, 2008).

To look more closely into the question of whether temperature and moisture interactions were significant in LIDET results, we performed an additional set of analyses of variance. We tested MAT, MAP, and their interaction to predict our decomposition model parameters  $k_S$ ,  $k_4$ ,  $S_{04}$ , and  $k_1$  in two-way ANOVAs across our entire set of litter  $\times$  site combinations. Interestingly, for

each of the three  $k$  constants, when the MAT  $\times$  MAP interaction term was included in the model it was significant ( $P < 0.02$ ), while MAT and MAP as direct effects were not significant.

#### *Biome-specific successes and biases*

Liski *et al.* (2003) made the important point that regression  $r^2$  values can be high, yet regression models can still exhibit systematic bias across an entire dataset or for particular regions or biomes. We examined this possibility by exploring graphs of our predicted vs. observed values of  $k_S$  and  $k_I$  for foliar litter for selected sites and sets of sites with climatic similarities. Predicted values of  $k_S$  and  $k_I$  derive from our best nonlinear regression equations using both climatic and litter quality variables [Table 4(a)]. For humid tropical sites, we found no systematic bias in modeled (i.e. predicted) values of the short-term constant  $k_S$  (Fig. 3a). We similarly found a lack of any such bias for  $k_S$  in temperate deciduous and coniferous forests and warm semi-deserts.

At the same time, we did find evidence of systematic bias in examining other biomes. Grouping temperate shortgrass steppe (CPR), prairie (KNZ), and temperate savanna (CDR) together as temperate grasslands, observed values of  $k_S$  tended to be systematically lower than predicted values (Fig. 3b). (A single exception, in which  $k_S$  was much higher than predicted by the regression, is shown by a single symbol in the far right of Fig. 3a and b; this is the tropical broadleaf litter *D. glauca*). This bias in the regression model over-predicting  $k_S$  also occurred in our dry tropical forest site (GSF). Together these results suggest that our regression approach over-predicted values of  $k_S$  in relatively arid or seasonally dry ecosystems. It is possible that in arid or seasonally dry systems, low humidity together with pulsed periods of rainfall produce wetting and drying cycles, the effects of which are not well captured in calculations of AET or CDI. Interestingly, in our results this was not an issue for warm deserts.

Others have suggested that the use of seasonal climate information, perhaps including a drought index that compares summer precipitation and PET, is needed (Trofymow *et al.*, 2002; Liski *et al.*, 2003). In our analysis the CDI, while used here on an annual basis, does employ seasonal climate information in its calculation. In further work it might be useful to compare the CDI approach with seasonal climate indices, but it was beyond our scope here.

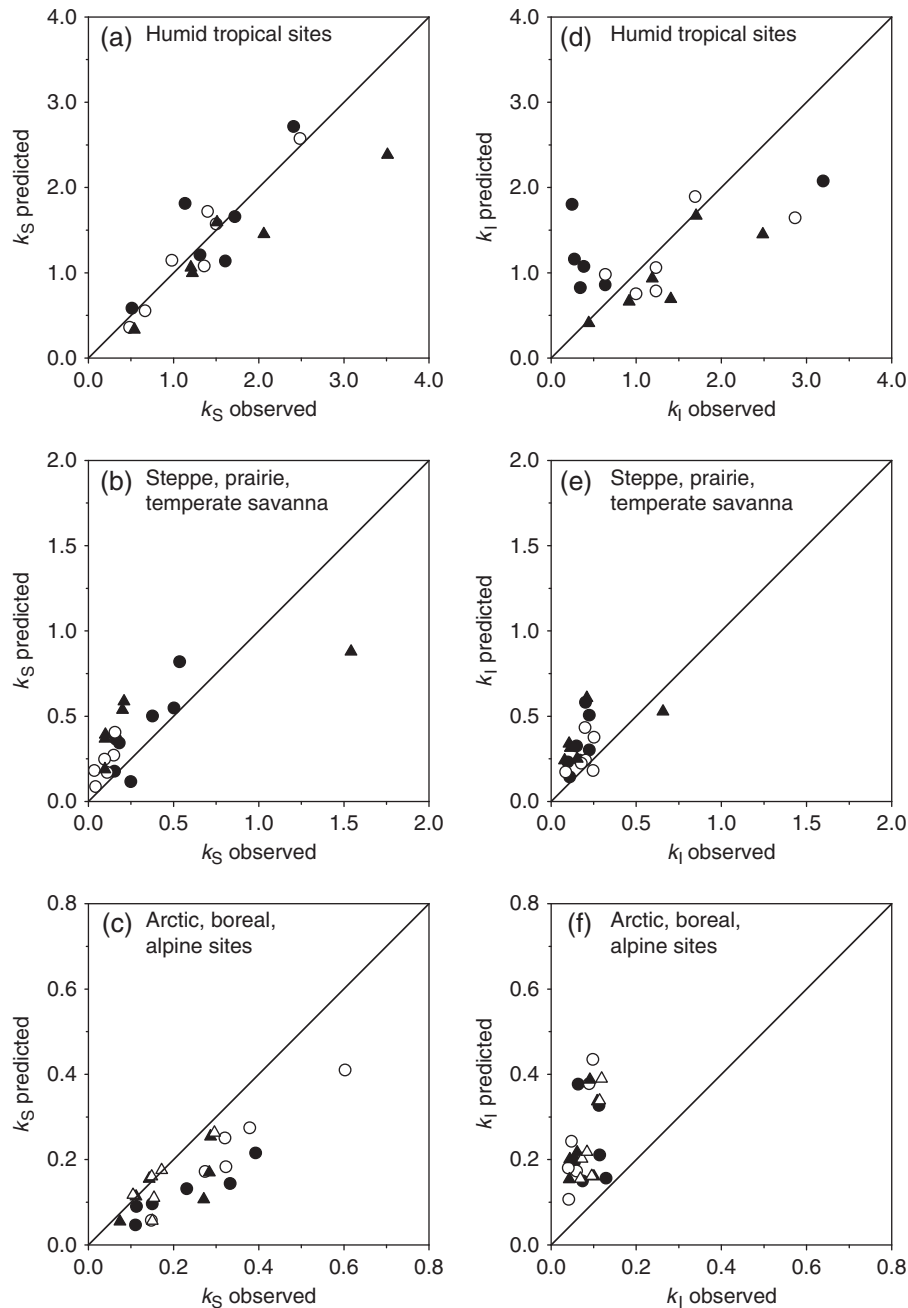
Because the regression approach captures the centroid in the dataset overall, if a group of sites tends to have  $k_S$  under-predicted, there must be other cases in which  $k_S$  is over-predicted. This occurred in the cold

sites: the arctic, boreal, and alpine ecosystems (Fig. 3c). Where MAT was 1.6 °C or lower, our best regression models underestimated rates of short-term decomposition. Decomposition proceeded at rates greater than those predicted by our regression equations. Possibly, litter layers themselves, or snow atop litter layers, insulated the litters from cold air temperatures and allowed decomposition to continue during cold months.

#### *Loss of predictability in later stages of decomposition*

A goal of the present analysis was to assess whether the basic elements of the Meentemeyer (1978) paradigm for controls on decomposition rate parameters could be extended to greater ranges of litter quality and climate and to the decadal time scale. We can conclude that for short-term (first-year) litter decomposition the paradigm can be extended, in its broad principles, to much greater ranges of climate and litter quality and even to novel combinations of climate and litter quality. Broad climatic variables that combined temperature and moisture, together with a continuous index of litter quality similar to the one used by Meentemeyer (1978) performed well in regressions for short-term  $k$  constants in the LIDET dataset. Analysis of variance showed significant climate and litter quality interactions (Table 5). Graphs of  $k_S$  values vs. AUF:N (Fig. 2) for multiple litters incubated at a site showed, at many sites, the predicted decline in  $k_S$  with increasing AUF:N (similar to Meentemeyer's decline of first-year  $k$  values with increasing litter lignin content). However, this paradigm cannot be extended with much predictive success to the decadal time scale.

Decadal scale decomposition parameters, including the stable fraction  $S_{04}$ , were simply much less predictable from annual climate and initial litter quality variables than were short-term decomposition parameters. Few other studies have empirically examined the controls on short- vs. long-term decomposition. In the CIDET study, Trofymow *et al.* (2002) found that overall predictability of regression models changed little from one to six years ( $r^2 = 0.76$  vs. 0.71, respectively), with ca. 30% to 55% initial mass remaining, in contrast with our results in which overall predictability declined dramatically after about 50% of the mass was lost. Trofymow *et al.* (2002) also found the AUF:N ratio to increase in predictive importance over time, whereas we found it to decline in predictive ability. In a study of decomposition of various plant materials in a single soil, de Haan (1977, cited in Berg, 1986) found much more scatter after 10 years, relative to 1 year, in the relationship between litter AUF and the amount of stable-phase material produced (similar to our stable asymptote  $S_{04}$ ).



**Fig. 3** Predicted vs. observed values of  $k_S$  ( $\text{year}^{-1}$ ) and  $k_I$  ( $\text{year}^{-1}$ ) for foliar litter for selected groups of sites; 1:1 lines are shown for reference. Predicted values of  $k_S$  and  $k_I$  derive from the best nonlinear regressions using climate and litter quality variables for foliar litter [Table 4(a)]. (a)  $k_S$  for humid tropical sites (● LBS, ○ LUQ, ▲ BCI); (b)  $k_S$  for temperate shortgrass steppe, prairie, and temperate savanna (● CDR, ○ CPR, ▲ KNZ); (c)  $k_S$  for arctic, boreal, and alpine sites (● ARC, ○ LVW, ▲ NWT, △ BNZ); (d)  $k_I$  for humid tropical sites [sites and symbols as in (a)]; (e)  $k_I$  for temperate shortgrass steppe, prairie, and temperate savanna [sites and symbols as in (b)]; (f)  $k_I$  for arctic, boreal, and alpine sites [sites and symbols as in (c)].

Our exploration of predicted vs. observed values of  $k_I$  for foliar litter (Fig. 3) offers additional insights. For grassland sites,  $k_I$  values continued to be under-predicted as with  $k_S$  (Fig. 3b and e). But in the arctic, boreal, and alpine sites, decadal-scale  $k_I$  values were over-

predicted by the regression approach (Fig. 3f), in stark contrast to the under-prediction of  $k_S$  values. For the  $k_I$  model over the dataset as a whole, there was a general bias of over-predicting values of  $k_I$  when they were low (as in cold sites), and under-predicting them when they

were high. In other words, the predicted range of  $k_1$  was much smaller than its observed range. The regression approach, when used with initial litter chemistry and annual averages in climate data, was not sensitive enough to capture large differences in decomposition over the longer time scale. Stated differently, these independent variables did not contain the right variances to capture the variance in  $k_1$  values across the set of 171 foliar litter  $\times$  site combinations. This is illustrated in humid tropical forests, where predictability of  $k_3$  was high and lacked bias (Fig. 3a). For  $k_1$  (Fig. 3d), the regression model overpredicted  $k_1$  values when they were below  $0.8 \text{ years}^{-1}$ , underpredicted higher observed values, and produced too narrow a range of  $k_1$  overall.

Aerts (1997) wrote that while caution should be used in extending the principles that control short-term decomposition to the long-term, there was no reason to expect that climatic controls on decomposition should differ from the first year to the long-term. However, our 10-year results now contradict that idea. Principles describing long-term decomposition are likely to require conceptual models of litter-ecosystem interactions that include additional factors. Properties of soils such as texture, water holding capacity, or pH (Hobbie & Gough, 2004) may be important in some types of ecosystems. The presence of direct sunlight striking decomposing litter may be important in some arid or semi-arid systems, as well as pulsed nature of precipitation events rather than average annual totals (Austin *et al.*, 2004; Parton *et al.*, 2007). Differences in the availability of exogenous nutrients such as N, phosphorus, or manganese may be important in some systems or regions (Meentemeyer and Berg, 1986; Berg *et al.*, 2000). Various exclusion studies (physical or chemical) or comparisons of tethered litter vs. litter in bags has also indicated that the suite of organisms decomposing litter could have major impacts on decomposition rates (Kurcheva, 1960; Witkamp & Olson, 1963; Witkamp & Crossley, 1966). The biotic environment also includes soil flora, soil fauna, and activities of particular classes of enzymes (DeForest *et al.*, 2004).

One of the most intriguing and potentially important factors not considered in our analysis is the chemical properties of other litter surrounding, or overtopping, the litter enclosed in litter bags in the field. Over the long-term, a particular litter becomes embedded in the chemical and biotic environment created by native litter, as the native litter continues to be added to the soil surface. In our study, as a litter bag became buried in native litter, it would be repeatedly exposed to organic leachates from the native litters, including waxes, oils, WSCarb, tannins and other polyphenols (McClaugherty, 1983), as well as secondary compounds

produced through decomposition of the overlying native litter (Qualls *et al.*, 1991; Guggenberger & Zech, 1994). The questions of whether mixture with other types of litter might regulate the decomposition processes taking place in a particular litter is a longstanding question in ecosystem biogeochemistry (Thomas, 1968; McClaugherty *et al.*, 1985).

The next generation of long-term decomposition studies should include methodological improvements as well as shifts in focus. Methodological improvements could include isotopic labeling to obviate the need to enclose litter in mesh litterbags (Hart, 1990; Bird & Torn, 2006). An important area for increased focus is to examine processes controlling the formation of the late-stage stable phase of litter and on the potentially very slow rate of decomposition of this material. These processes are important to understand as controls on ecosystem carbon storage and carbon balance.

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