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Controls on long-term root and leaf litter decomposition in neotropical forests

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Abstract

Litter decomposition represents one of the largest annual fluxes of carbon (C) from terrestrial ecosystems, particularly for tropical forests, which are generally characterized by high net primary productivity and litter turnover. We used data from the Long-Term Intersite Decomposition Experiment (LIDET) to (1) determine the relative importance of climate and litter quality as predictors of decomposition rates, (2) compare patterns in root and leaf litter decomposition, (3) identify controls on net nitrogen (N) release during decay, and (4) compare LIDET rates with native species studies across five bioclimatically diverse neotropical forests. Leaf and root litter decomposed fastest in the lower montane rain and moist forests and slowest in the seasonally dry forest. The single best predictor of leaf litter decomposition was the climate decomposition index (CDI), explaining 51% of the variability across all sites. The strongest models for predicting leaf decomposition combined climate and litter chemistry, and included CDI and lignin ($R^2 = 0.69$), or CDI, N and nonpolar extractives ($R^2 = 0.69$). While we found no significant differences in decomposition rates between leaf and root litter, drivers of decomposition differed for the two tissue types. Initial stages of decomposition, determined as the time to 50% mass remaining, were driven primarily by precipitation for leaf litter ($R^2 = 0.93$) and by temperature for root litter ($R^2 = 0.86$). The rate of N release from leaf litter was positively correlated with initial N concentrations; net N immobilization increased with decreasing initial N concentrations. This study demonstrates that decomposition is sensitive to climate within and across tropical forests. Our results suggest that climate change and increasing N deposition in tropical forests are likely to result in significant changes to decomposition rates in this biome.

Keywords: climate, LIDET, lignin, nitrogen, substrate quality, tropical

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Introduction

The tropical forest biome is characterized by rapid decomposition rates (Parton *et al*., 2007; Adair *et al*., 2008). This fast decomposition, when coupled with typically high net primary productivity (NPP) (Melillo *et al*., 1993), leads to some of the largest annual carbon (C) fluxes as carbon dioxide (CO_2) from terrestrial ecosystems globally (Raich & Schlesinger, 1992). Litter decomposition also plays an important role in nutrient cycling in tropical forests by mineralizing and releasing nutrients for plant and microbial uptake. This is particularly important for tropical forests on highly weathered soils, which typically have low nutrient-holding capacity (Sanchez, 1976). The majority of litter decomposition studies conducted in the tropics have used one site, one life zone, and/or native litters only (see Cuevas & Medina, 1988). While these studies are important for determining local rates and controls on decomposition, they are less useful for identifying broad regional or biome-scale trends in decomposition.

Climate and litter chemistry are thought to be the primary drivers of decomposition in temperate ecosystems (Meentemeyer, 1978a), but similar analyses are lacking for tropical forests. A model used to predict decomposition for

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the entire Long-Term Intersite Decomposition Experiment (LIDET) dataset, including 28 sites across multiple biomes (Adair *et al*., 2008), suggested unique controls on decomposition in tropical ecosystems. Climate indices that incorporate both temperature and precipitation, such as actual evapotranspiration (AET) and the climate decomposition index (CDI) (*sensu* Parton *et al*., 1994), are generally the best predictors of decomposition at regional and global scales (Meentemeyer, 1978a, b; Aerts, 1997; Gholz *et al*., 2000; Parton *et al*., 2007). Temperatures in the tropics tend to be warmer and relatively constant compared with temperate regions. Consistent moderate to high temperatures create conditions favorable for decomposers (Vitousek, 1984; Schlesinger & Andrews, 2000), but the lack of strong seasonality in temperature may decrease its value as a predictor of decomposition rates within the tropical biome.

In contrast to temperature, rainfall in tropical forests varies widely, ranging from as little as 500 mm to as much as >5000 mm annually (Holdridge *et al*., 1971). Seasonality of rainfall is also highly variable across the tropics (Austin & Vitousek, 2000). Decomposition in very wet tropical forests or during wet periods may be inhibited by low oxygen availability (McGroddy & Silver, 2000; Schuur, 2001), whereas seasonal drought in dry and mesic tropical forests can also slow decomposition rates (Goulden *et al*., 2004). The wider range of precipitation relative to temperature may make precipitation a better predictor of decomposition in tropical regions. However, climate controls on leaf litter decomposition may differ from those of root decomposition. Foliar tissues generally decompose on the soil surface where they are directly exposed to rainfall and throughfall, and subject to desiccation. Root tissues occurring in the mineral soil are likely to be more buffered from the direct effects of climate (Silver & Miya, 2001).

Litter chemistry has been shown to be an important driver of decomposition and litter nutrient release in the tropics (Loranger *et al*., 2002; Arunachalam & Singh, 2004; Goma-Tchimbakala & Bernhard-Reversat, 2006). Typical litter chemistry indices include the initial tissue N or lignin concentrations, the lignin : N or C : N ratios, and tannin and polyphenolic concentrations (McClaugherty & Berg, 1987; Ryan *et al*., 1990). The importance of tissue chemistry may differ for leaf and root litter decomposition, because of the differences in microbial decomposer communities on the surface vs. in the soil (Bills & Polishook, 1994; Tiwari *et al*., 1994; Silver, 1998; Chen *et al*., 2001) or to other differences in microbial community and activity (Gonzalez & Seastedt, 2001; Carney & Matson, 2005). Initial litter chemistry not only affects rates of mass loss, but can also determine rates of nutrient immobilization and mineralization (Scott & Binkley, 1997). Nitrogen concentrations commonly increase in decomposing litter as decomposers colonize and degrade litter (Gosz *et al*., 1973), fix N_2 (Wood, 1974), or transport N from soils to litter via fungal hyphae (Wood, 1974). The extent of net N immobilization is often related to the initial N concentration of the decomposing litter (Aber & Melillo, 1980; Melillo *et al*., 1982), whereas N mineralization in soils has been shown to correlate with litter lignin concentrations (Scott & Binkley, 1997).

In this study we used data from the tropical forest LIDET sites to address four key questions regarding patterns and controls on litter decomposition in the tropical forest biome. First, we asked what the relative importance of climate and litter chemistry is in tropical forest litter decomposition. We predicted that precipitation and litter chemistry would be the dominant drivers of decomposition in the tropics, because of the near constant favorable temperatures of this biome. Second, we asked if the drivers of leaf litter decomposition differ from those of root litter decomposition in tropical forests. We expected that root tissue would be best predicted by initial litter chemistry, because roots are relatively buffered from the direct effects of climate by their location in soils. Leaf tissue decomposition is more likely to be correlated with climate (and particularly precipitation) based on previous temperate zone studies and global analyses (Meentemeyer, 1978a; Aerts, 1997; Silver & Miya, 2001). Third, we examined potential drivers of patterns in net N mineralization and immobilization during decomposition across tropical forests. High soil N typical of tropical forest soils (Vitousek & Howarth, 1991; Hobbie & Vitousek, 2000) could decrease the occurrence of N immobilization across litter types. Finally, to determine if the patterns we observed with the nine LIDET standard litter types are representative of decomposition rates of native litter species and localized climate gradients, we compared our results with independent published datasets from the tropical LIDET sites and additional decomposition studies in Hawaii.

Materials and methods

The five tropical forest LIDET sites included a lowland moist forest at Barro Colorado Island, Panama (BCI), a lowland dry forest at Guanica State Forest, Puerto Rico (GSF), a lowland wet forest at La Selva Biological Station, Costa Rica (LBS), a lower montane wet forest at the Luquillo Experimental Forest, Puerto Rico (LUQ), and a montane cloud forest at Monteverde, Costa Rica (MTV). These tropical forests span a wide range of tropical climate characteristics (Table 1).

We used data from five leaf litter species that were decomposed at all sites: sugar maple (*Acer saccharum*, ACSA), a tropical hardwood (*Drypetes glauca*, DRGL), chestnut oak (*Quercus prinus*, QUPR), western red cedar

Table 1 Study site characteristics and litter species decomposed

Site	Location (latitude, longitude)	Tropical forest type	MAT* (°C)	MAP* (mm)	Leaf species decomposed†	Root species decomposed†
Barro Colorado Island (BCI)	Panama (9°10′N, 79°51′W)	Lowland moist	27.2	2692	ACSA, DRGL, PIEL, QUPR, THPL, TRAE	ANGE, DRGL, PIEL
Guanica State Forest (GSF)	Puerto Rico (17°57′N, 65°52′W)	Dry	26.4	508	ACSA, DRGL, PIEL, QUPR, THPL, TRAE	ANGE, DRGL, PIRE
La Selva Biological Station (LBS)	Costa Rica (10°25′N, 84°1′W)	Lowland wet	26.2	4100	ACSA, DRGL, PIRE, QUPR, THPL, TRAE	ANGE, DRGL, PIEL
Luquillo Experimental Forest (LUQ)	Puerto Rico (18°18′N, 5°49′W)	Lower montane wet	23.5	3363	ACSA, DRGL, PIRE, QUPR, THPL, TRAE	ANGE, DRGL, PIEL
Monteverde (MTV)	Costa Rica (10°18′N, 84°48′W)	Cloud	17.7	2685	ACSA, DRGL, PIEL, QUPR, THPL, TRAE	ANGE, DRGL, PIRE

*Averaged over the 10-year Long-Term Intersite Decomposition Experiment (LIDET) study period (1990–2000).
†*Andropogon gerardii* (ANGE), *Acer saccharum* (ACSA), *Drypetes glauca* (DRGL), *Pinus elliottii* (PIEL), *Pinus resinosa* (PIRE), *Quercus prinus* (QUPR), *Thuja plicata* (THPL), *Triticum aestivum* (TRAE).

(*Thuja plicata*, THPL), and wheat (*Triticum aestivum*, TRAE). An additional pine needle litter was decomposed at each site. Red pine (*Pinus resinosa*, PIRE) was used at LBS and LUQ, and slash pine (*Pinus elliottii*, PIEL) was used at BCI, GSF and MTV. Three root litter species were decomposed at each site, including big bluestem (*Andropogon gerardii*, ANGE), DRGL, and either PIRE (at GSF and MTV) or PIEL (at BCI, LBS and LUQ) (Table 1). These species were chosen to provide a range in N concentrations, lignin : N, and lignin concentrations.

Details of the field and laboratory protocols can be found at http://www.fsl.orst.edu/lter/research/intersite/lidet/lidet_meth/lidet.htm and in Gholz *et al*. (2000). Briefly, litter was collected from senescing plants (temperate species) or collected green (tropical species DRGL). All litter species were air-dried at ambient temperatures except DRGL, which was oven-dried at 40 °C. Litter used at sites in Costa Rica was sterilized using gamma radiation to meet import requirements. Litterbags (20 cm × 20 cm, mesh sizes 1 mm for leaves, 0.1 mm for roots) were filled with ~10 g dry weight of leaf litter (placed aboveground), or 5–7 g dry weight of fine roots (inserted into surface soils). Replicate litterbags were placed in four locations at each site in 1990 or 1991, and collected at multiple time points for up to 10 years. Final time points were earlier for tropical sites (1.8–5 years) than for most temperate sites because of rapid decomposition. The mass remaining (ash-free weight) was averaged for each harvest date across the four replicates per species and tissue type.

Climate parameters

We tested four climate indices as predictors of decomposition: mean annual precipitation (MAP, mm), mean annual air temperature (MAT, °C), AET (mm), and the CDI, which incorporates the seasonality of rainfall and temperature in an integrated index to predict decomposition (Parton *et al*., 2007). The mean annual values for these variables were calculated using the observed weather during the 10-year experimental period near the study sites (1990–2000). The monthly water budget in the Century model (Parton *et al*., 1994) was used to calculate AET from potential evapotranspiration rates (PET) at each site, using observed monthly average maximum and minimum air temperature and monthly precipitation.

Tissue chemistry measurements

After collection, litterbags were oven-dried at 55 °C until mass stabilized. Harvested samples were pooled within species, site, and time for chemical analyses. All chemical analyses were performed at Oregon State

University using the following methods. (1) All initial samples were analyzed for total ash in a muffle furnace and for C and N concentrations on an elemental analyzer. Initial tissue samples were also analyzed for Kjeldahl N and proximate C fractions, including Klason lignin (hereafter lignin), tannins, nonpolar extractives, water-soluble extractives, and acid-soluble extractives (Ryan *et al*., 1990). (2) For the decomposed samples, approximately 25% of pooled samples were analyzed for ash, C, and N concentrations. The other chemical characteristics listed above were predicted for the decomposed samples using near infrared reflectance spectroscopy (LIDET, 1995).

Calculation of decomposition rate constants

We considered single-phase, two-phase, and lag-phase models to calculate decomposition rate constants for mass loss over time. The single-phase model represents tissue that decomposes as a uniform pool of C. The two-phase model describes litter that has a labile, quickly decomposing C pool and a recalcitrant, slowly decomposing C pool. The lag-phase model represents litter that is not immediately decomposed presumably because of a lag in colonization by decomposers. We fit every combination of site, species, and tissue type (leaf or root) with each of the three models. Models were considered biologically realistic if the resulting curve fit (i.e., mass remaining vs. time) had a *Y*-intercept value between 95% and 105% initial mass; this range was chosen to allow for inherent variability in this diverse dataset. A two-phase model was used for data subsets with *Y*-intercepts below 95% mass at time zero, under the assumption that a rapid early phase of decomposition occurred before the first harvest date. The lag-phase model did not fit any of our data subsets and thus was not used here. We evaluated data for outliers and rejected 1 out of 349 data points.

Using either a single- or two-phase approach, we calculated the integrated, weighted-average decomposition rate (Olson, 1963; Harmon *et al*., 1990) as a measure of average long-term decomposition. This calculation is based on the predicted mass remaining (M_R) for sequential time points, where the sum of mass remaining for all time points represents the hypothetical steady-state of forest floor mass, and mass input is 100 units:

$$k_I = \frac{100}{\sum M_{R(t0-200)}}, \quad (1)$$

where k_I is the time-integrated average decomposition rate constant and $\sum M_R$ represents the sum of mass remaining for all time points from 0 to 200 years of decomposition. We used a 0.1-year time step for this numerical integration procedure.

The value of M_R for each time point in both the single- and two-phase models was estimated using exponential decay equations for observed data. For the single-phase model, mass remaining at each time point was calculated as:

$$M_R = M_0 \times e^{-k(t)}, \quad (2)$$

where M_0 is the mass at time zero (100 units), k is the decomposition rate constant (estimated as the slope of a log-linear regression), and t is time. For the two-phase model, mass remaining at each time point was calculated as:

$$M_R = M_s \times e^{-ks(t)} + M_f \times e^{-kf(t)}, \quad (3)$$

where M_s is the initial mass of the slow pool and k_s is the decomposition rate constant of the slow pool of C. We assumed that the log-linear curve fit of observed data represented decomposition of the slow pool for datasets with *Y*-intercept $<95\%$ mass. Thus, parameters for the slow pool were estimated as $M_s = Y$-intercept, and k_s = slope of a log-linear fit of the observed data. The parameters M_f and k_f are the initial mass and decomposition rate constant of the fast pool of C, where

$$M_f = 100 - M_s, \quad (4)$$

To estimate k_f, we assumed that 95% of the fast pool had been decomposed by the time of the first litter harvest (t_{p1}) such that

$$k_f = \frac{\ln 0.95}{t_{p1}}. \quad (5)$$

We also tested nonlinear equations to calculate M_R for each time step in these two models, but doing so did not significantly change our calculations of k_I. The two-phase integrated model best described decomposition rates of both root and leaf litter at most sites and for most species. An exception was leaf litter decomposition at GSF, where overall leaf decomposition was best described by a single-phase integrated model. At the species level, decomposition of PIEL leaves and PIRE roots was best described using the single-phase model. Across all combinations of site, species and tissue type, 70% of leaf litter data and 73% of root data were best described using a two-phase model. Remaining combinations were described using a single-phase model.

The two-phase or single-phase time-integrated rate constants (k_I in above equations, hereafter *k*-values) for each site, species, and tissue type combination were used in our subsequent analyses. We also estimated the time to reach 50% of the original mass remaining (in years) for each site using the time-integrated model described above with the single- or two-phase model,

as appropriate. We used time to 50% mass remaining as an index of the early stages of decomposition.

Statistical analyses

Statistical analyses were performed using JMP 5.0 (SAS Institute Inc., Cary, NC, USA) and SYSTAT 10 (SSI, Richmond, CA, USA). Statistical significance was determined at the 95% level for all tests unless otherwise noted. Data were log-transformed when necessary to meet the normality assumptions for analysis of variance (ANOVA). To address our first question regarding the relative importance of climate vs. litter chemistry in tropical decomposition, differences in leaf and root *k*-values across the climatically distinct sites and chemically distinct species were determined with ANOVA and the least significant differences (LSD) means separation test. For question one, we also used backwards stepwise multiple linear regressions, in which all independent parameters were included in the regression model first, and removed sequentially if not significant. This approach determine the best climate and litter chemistry variables for predicting decomposition across tropical sites and species, and to compare controls on decomposition at the tropical LIDET sites with controls observed in the global LIDET dataset (Currie *et al*., in review). Climate parameters included CDI, AET, MAT, and MAP. Litter chemical indices included initial N, C : N, lignin : N, lignin, tannins, nonpolar extractives, water-soluble extractives, and acid-soluble extractives. By analyzing leaf and root litter data separately in these analyses, we were able to determine if the drivers of leaf and root decomposition were different (question two). Average leaf and root *k*-values across sites and species were also compared using a Student's *t*-test.

Because *Pinus* litter species differed across sites, we excluded this genus from site-level analyses. Additional regressions were run for the three sites with PIEL leaves and roots, and included the other five species. All analyses were repeated using the time to 50% mass remaining as the response variable to identify differences in controls on short-term vs. time-integrated decomposition.

To investigate the drivers of N mineralization and immobilization during decomposition (question three), we used the model developed by Parton *et al*. (2007) to explore patterns in N dynamics for leaf litter, and we used linear models for root litter. The model (Parton *et al*., 2007) describes N concentrations during decomposition as a function of observed mass remaining and initial N concentrations, and accurately described leaf decomposition for the global LIDET dataset. Root litter has been observed to release N linearly with decomposition regardless of species or location (Parton *et al*., 2007). To identify factors other than mass loss that drive N release from root litter, we used linear regressions with %N remaining as the response factor, and total mass remaining plus the above climate and tissues chemistry factors as independent variables. All root litter species from all sites were included in these analyses.

To determine whether patterns observed using the LIDET litters were representative of native litter decomposition (question four), we compiled a dataset of leaf litter *k*-values from this study and from independent (non-LIDET) native species decomposition studies at the five tropical LIDET sites and Hawaii, where extensive research on tropical decomposition has been conducted. We regressed these compiled *k*-values against MAP and MAT to determine whether there were different trends for native litter studies compared with LIDET litter species.

Results

Patterns in leaf and root litter decomposition

Over the 10-year study period, LBS had the highest rainfall, AET, and CDI, while GSF had the lowest. BCI was the warmest site, and MTV was the coolest site (Tables 1 and 2). Leaf litter *k*-values ranged from 0.26 to 1.27 per year across sites (Table 2) and from 0.27 to 1.37 per year across species (Table 3). Root litter *k*-values ranged from 0.42 to 1.06 per year across sites (Table 2) and 0.33 to 0.94 per year across species (Table 3). Among sites, leaf mass loss was slowest at GSF (the one site with single-phase decomposition), and fastest at LUQ and BCI (Fig. 1). The proportion of leaf litter mass calculated to be in the fast decomposition pool was 25% (BCI), 50% (LBS), 29% (LUQ), and 42% (MTV). Root mass loss was also slowest at GSF and fastest at LUQ (Table 2). The proportion of root litter in the fast pool was 25% (BCI), 17% (GSF), 27% (LBS), 6% (LUQ), and 18% (MTV).

Among species, leaf mass loss was slowest for PIEL (the species with highest lignin : N and C : N) and fastest for DRGL (highest %N); root mass loss was slowest for PIRE and fastest for ANGE (the single grass species, Table 3). Site, species, and tissue type (leaf or root) were all significant factors for describing variability in *k*-values. However, tissue type was only a significant factor when species was also included in the analysis. On average there was no significant difference between leaf and root *k*-values. Within tissue type (roots or leaves), *k* differed significantly among sites and species (Fig. 1).

Climate and chemical predictors of decomposition rates

Climate factors were the best single predictors of decomposition rates for leaf litter across all sites and species (Table 4). The single best predictor of leaf litter

Table 2 Site-level climate parameters and litter decomposition rates (mean ± SE)

Site	AET (mm)	CDI	Leaf *k*-value (per year)*	Leaf $t_{0.5}$ (year)‡	Root *k*-value (per year)	Root $t_{0.5}$ (year)‡
BCI	1368	0.78	1.27 ± 0.30 a	0.45	0.81 ± 0.26 ab	0.60
GSF	503	0.39	0.26 ± 0.06† b	2.00	0.42 ± 0.07 b	0.75
LBS	1699	0.89	0.65 ± 0.10 b	0.15	0.62 ± 0.14 ab	0.80
LUQ	1234	0.84	1.22 ± 0.24 a	0.40	1.06 ± 0.28 a	0.75
MTV	1084	0.60	0.47 ± 0.06 b	0.60	0.50 ± 0.08 ab	1.15

*Time-integrated decomposition rate constants calculated separately for each species (Appendix A) were averaged to obtain mean site-level *k*-values. Letters indicate differences in *k*-values within leaf or root tissues among sites using an LSD test.
†A two-phase time-integrated decomposition model best described decomposition of all species, except for GSF leaves, which were best described by a single-phase model.
‡$t_{0.5}$: time to 50% mass remaining.

Table 3 Species-level chemical parameters* and litter decomposition rates (mean ± SE)†

Tissue type	Species	N (%)*	C : N	Lignin : N	Lignin (%)	Nonpolar extractives (%)	Tannins (%)	Water-soluble carbohydrates (%)	Acid-soluble carbohydrates (%)	*k*-value (per year)‡	$t_{0.5}$ (year)§
Leaf	ACSA	0.81	61.8	19.7	15.9	8.2	7.7	11.1	12.7	0.77 ± 0.21 ab	0.70
	DRGL	**1.97**	24.2	5.5	10.9	8.0	**8.0**	**13.3**	18.1	1.37 ± 0.42 a	0.08
	PIEL	0.36	**150.7**	**59.5**	21.4	**17.3**	4.5	6.8	20.3	0.27 ± 0.09 b	3.28
	PIRE	0.59	90.9	32.6	19.2	15.3	7.4	9.8	20.1	0.54 ± 0.11 b	1.20
	QUPR	1.03	50.1	22.9	23.5	9.3	6.9	7.1	18.0	0.62 ± 0.17 b	0.80
	THPL	0.62	82.1	42.8	**26.7**	14.0	3.0	7.8	17.3	0.56 ± 0.16 ab	1.10
	TRAE	0.38	125.3	42.9	16.2	3.4	2.9	5.0	**41.1**	0.96 ± 0.23 ab	0.30
Root	ANGE	0.63	58.7	16.7	10.5	5.9	1.1	5.3	**33.2**	0.94 ± 0.19 a	0.50
	DRGL	0.76	**63.5**	21.2	16.1	**10.6**	2.4	6.7	15.3	0.73 ± 0.12 ab	0.80
	PIEL	0.82	60.4	**42.7**	**34.9**	8.9	**3.3**	**8.5**	19.7	0.42 ± 0.09 b	1.60
	PIRE	**1.22**	39.9	23.2	28.2	6.1	2.3	2.2	13.3	0.33 ± 0.02 b	2.00

*Several chemical parameters were weakly autocorrelated, including N and tannins ($R^2 = 0.31$), N and acid-soluble carbohydrate ($R^2 = 0.17$), N and water-soluble carbohydrates ($R^2 = 0.38$), lignin and nonpolar extractives ($R^2 = 0.14$), lignin and acid-soluble carbohydrates ($R^2 = 0.10$), nonpolar extractives and acid-soluble carbohydrates ($R^2 = 0.30$), tannins and acid-soluble carbohydrates ($R^2 = 0.22$), tannins and water-soluble carbohydrates ($R^2 = 0.63$), and acid-soluble and water-soluble carbohydrates ($R^2 = 0.22$). Bolded text indicates the highest leaf and root values for each chemical parameter.
†A two-phase time-integrated decomposition model best described decomposition of all species and tissue types, except PIEL leaves and PIRE roots for which a single-phase model was more suitable. Time-integrated decomposition rate constants calculated separately for each site, species and type (Appendix A) were averaged to obtain mean species-level *k*-values.
‡Letters indicate differences in *k*-values within each tissue type (root and leaf) using LSD tests.
§$t_{0.5}$: time to 50% mass remaining.

decomposition was CDI ($R^2 = 0.51$; $R^2 = 0.63$ across the three sites that included PIEL). The best multiple regressions for predicting leaf litter decomposition across sites combined CDI and lignin, or CDI, initial N, and nonpolar extractives ($R^2 = 0.69$ for both combinations). For sites with PIEL litter, a multiple regression with CDI, initial N, and nonpolar extractives was the best model for predicting leaf litter decomposition rates ($R^2 = 0.93$). As expected, temperature was generally not a good predictor of decomposition rates for leaf litter (Table 4).

Results for regressions using time to 50% mass remaining as the response variable were similar to results using *k*-values. In general, R^2 values increased for leaf litter decomposition when using time to 50% mass remaining across sites, with climate as the strongest predictor (Table 4). For leaf litter, site-average time to 50% mass remaining was significantly positively correlated with MAP ($R^2 = 0.93$), CDI ($R^2 = 0.86$), and AET ($R^2 = 0.89$, Fig. 2a–c). The strong influence of GSF is seen in the correlation between time to 50% mass remaining and precipitation, CDI, and AET (Fig. 2a–c).

The single best predictor for root decomposition rates across the three sites that included PIEL was lignin concentration ($R^2 = 0.77$). AET improved the predictive power of regressions at the sites with PIEL root litter

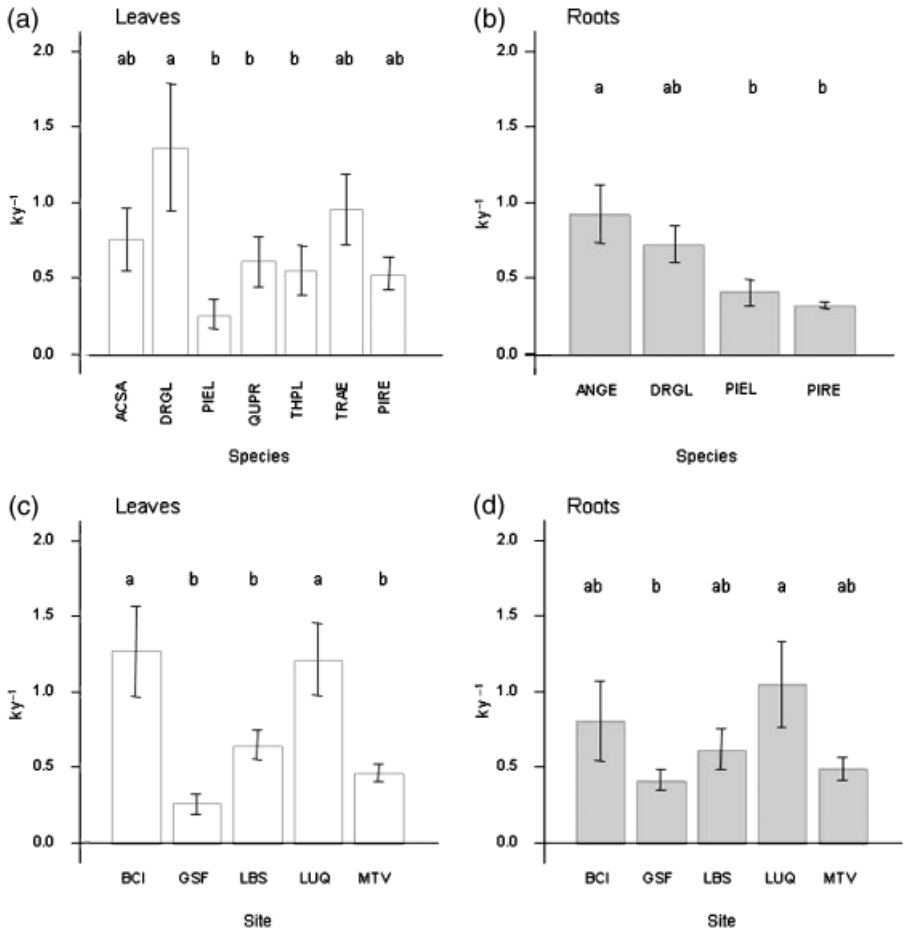

Fig. 1 Decomposition rate constants for (a) leaves and (b) roots compared by species, and for (c) leaves and (d) roots compared by site. Letters represent significant differences in *k*-values among sites or species using least significant difference (LSD) tests ($P < 0.05$).

($R^2 = 0.91$ when combined with lignin). Similarly, we found good relationships in PIEL sites decomposition rates with AET, initial N, and nonpolar extractives ($R^2 = 0.91$), or AET, initial N, and tannins ($R^2 = 0.91$). In contrast to analyses with leaf litter, temperature was a significant factor in some of the multiple regressions for sites including PIEL root litter. As with leaf litter, analyses using time to 50% mass remaining often had greater predictive power than those using *k*-values (Table 4). Using site-averaged values of time to 50% mass remaining, the initial phases of root decomposition were strongly positively correlated with MAT, with a strong influence of decomposition rates at MTV ($R^2 = 0.86$, Fig. 2d).

Litter nitrogen dynamics

Initial N concentrations were the best predictor of net N immobilization and release in leaves during decomposition. Net N immobilization during the early stages of decomposition was greatest for species with a low initial N concentration (Fig. 3a–f). The time to net N release (mineralization) was also greatest for species with low initial N concentrations. The two *Pinus* species (PIEL and PIRE) differed in their net N release patterns, reflecting different initial N concentrations. Net N release often occurred very late in the decomposition sequence, at approximately 40% of the initial mass remaining for N-poor TRAE. Comparing sites, leaf litter at BCI and LUQ exhibited earlier net N release, whereas GSF and MTV retained N for longer time periods, similar to patterns in mass loss (Fig. 3).

In contrast to leaf litter, net N release from roots followed a linear pattern, with little net N immobilization (Fig. 4). The best predictor of net N release from roots was mass remaining ($R^2 = 0.64$, Table 5). Adding C:N ($R^2 = 0.79$) or initial N and nonpolar extractives ($R^2 = 0.79$) improved the predictive power of the regression. Net N immobilization in root litter occurred only in DRGL, which

Table 4 Climate and chemical predictors of decomposition rates†

Climate factors	N parameter‡	Secondary C compounds‡,§	Leaf R^2 (all sites)	Leaf R^2 (PIEL sites)	Root R^2 (all sites)	Root R^2 (PIEL sites)
MAP	–	–	0.35/0.42	0.43/0.46	0.34*	ns
MAT	–	–	ns	ns	ns	ns
AET	–	–	0.36/0.41	0.59/0.51	0.32	ns
CDI	–	–	0.51/0.43	0.63/0.49	**0.58**¶/0.55	ns
–	N	–	ns	ns	ns	0.58/0.69
–	C : N	–	ns	ns	ns	ns
–	Lignin : N	–	ns	ns	ns	0.75/0.81
–	–	Lignin	ns/0.41	0.17*/0.36	ns	0.77/0.84
–	–	NPE	ns/0.18	0.25/ns	ns	ns
–	–	Tannins	ns	ns	ns	0.63/0.74
–	–	ASC	ns	ns	ns	ns
–	–	WSC	ns	ns	ns	0.72/0.83
–	N	NPE	ns/0.30	ns	ns	0.83*/0.85
–	N	ASC	ns/0.29	ns	ns	0.83*/0.85
MAP	N	–	0.26/0.52	0.55*/ns	ns	ns
MAP	Lignin : N	–	ns	0.57/ns	ns	ns
MAT	Lignin : N	–	ns	ns	ns	0.87/0.89
AET	N	–	ns/0.50	0.71/ns	ns	ns
AET	C : N	–	ns	0.68/ns	ns	ns
AET	Lignin : N	–	ns	0.73/ns	ns	0.90/ns
CDI	N	–	0.57*/0.53	0.75/ns	ns/0.76	ns/0.76
CDI	C : N	–	ns	0.72/ns	ns/0.76	ns/0.76
CDI	Lignin : N	–	ns	0.77/ns	ns/0.76	ns/0.76
MAP	–	Lignin	0.52/0.83	0.60/0.83	ns	ns
AET	–	Lignin	0.53/0.82	0.76/0.87	ns	**0.91**‖/ns
CDI	–	Lignin	**0.69****/0.84	0.80/0.86	ns/0.76	ns/0.76
MAP	–	NPE	0.45/0.60	0.68/0.52	ns	ns
AET	–	NPE	0.46/0.58	0.84/0.61	ns	ns
CDI	–	NPE	0.61	0.88/0.59	ns/0.76	ns/0.76
AET	–	Tannins	ns	ns	ns	0.78*/ns
MAT	–	WSC	ns	ns	ns	0.84*/0.90
AET	–	WSC	ns/0.50	ns	ns	0.87/0.89
MAP	N	NPE	0.52*/0.72	ns	Lost df	ns
MAT	N	NPE	ns	ns	Lost df	0.88/0.92
AET	N	NPE	0.53*/0.70	0.89/ns	Lost df	0.91/0.92
CDI	N	NPE	0.69/0.73	**0.93**††/ns	Lost df	ns
MAT	N	Tannins	ns	ns	Lost df	0.88/0.92
AET	N	Tannins	ns	ns	Lost df	0.91/0.92

†Time-integrated decomposition rates (k-values) and $t_{0.5}$ were regressed against climate and chemical factors. Where correlations differed, R^2 for k-value models are shown on the left and R^2 for $t_{0.5}$ models are shown on the right. All k-values for combinations of site, species and type were used in regressions, using natural log-transformed values. For regressions with all sites, PIEL and PIRE were excluded. For regressions with *Pinus*, BCI, GSF, and MTV were sites with PIEL leaves, and BCI, LBS, and LUQ were sites with PIEL roots. Nonsignificant (ns) indicates a nonsignificant model or nonsignificant model factor. Two-factor models not shown were not significant, and three-factor models not shown had nonsignificant factors. The simplest, most significant model for each group is shown in bold, and the equations for these are:

**[leaves, all sites] $\ln(k) = -0.05(\%\ \text{lignin}) + 2.8(\text{CDI}) - 1.4$.

††[leaves, PIEL sites] $\ln(k) = -0.08(\text{NPE}) + 0.3(\%\text{N}) + 4(\text{CDI}) - 2.6$.

¶[roots, all sites] $\ln(k) = 1.6(\text{CDI}) - 1.4$.

‖[roots, PIEL sites] $\ln(k) = -0.04(\%\ \text{lignin}) - 0.001(\text{AET}) + 2$.

‡Chemical properties are in percent.

§NPE, nonpolar extractives; ASC, acid-soluble carbohydrates; WSC, water-soluble carbohydrates.

*$P < 0.1$ for one factor. For all other factors and for regressions overall, $P < 0.05$.

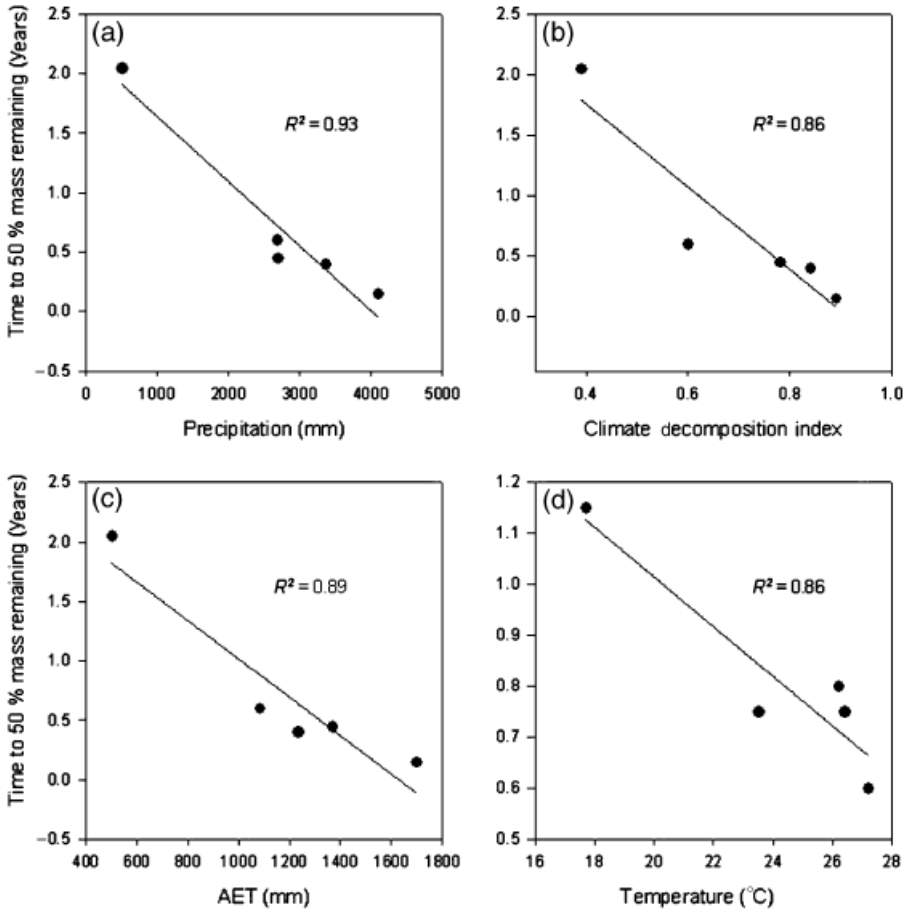

Fig. 2 Linear regression of $t_{0.5}$ against (a) mean annual precipitation (MAP) for leaves, (b) climate decomposition index (CDI) for leaves, (c) mean annual actual evapotranspiration (AET) rate for leaves, and (d) mean annual temperature (MAT) for roots ($P < 0.05$). The equations for the regressions are: (a) leaf $t_{0.5} = 2.183 - 0.0005 \times \text{MAP}$; (b) leaf $t_{0.5} = 3.123 - 3.419 \times \text{CDI}$; (c) leaf $t_{0.5} = 2.633 - 0.0016 \times \text{AET}$; (d) root $t_{0.5} = 1.988 - 0.0487 \times \text{MAT}$.

also had the highest nonpolar extractives (Fig. 4). Climate factors were correlated with mass loss and did not add further predictive power to regressions of net N release from roots.

Comparison with native litters

Decomposition rates in the LIDET study were similar to rates reported for native species decomposition at each site (Table 6, Fig. 5). The exception was LBS, which showed faster leaf litter decomposition rates for native species during two 1-year studies. We compared our compiled data with decomposition rates from two climate gradient studies in the Hawaiian Islands that showed contrasting trends of decomposition with precipitation (Austin & Vitousek, 2000; Schuur, 2001). Schuur (2001) reported decreasing leaf litter decomposition rates along a gradient of increasing annual rainfall. While LIDET decomposition rates were similar to rates observed by Schuur (2001), both the overall LIDET trend and the compiled dataset showed the opposite relationship: a significant positive correlation between MAP and leaf *k*-values ($R^2 = 0.43$ for the compiled dataset, Fig. 5). There were no significant relationships with MAT.

Discussion

Climate drivers of decomposition in tropical forests

Climate factors were the most important drivers of leaf and root decomposition across the five tropical sites in this study. In our multiple linear regressions, the single best predictor of leaf and root decomposition rates across all combinations of site and litter type was CDI. For the three sites with PIEL leaf litter, CDI was also the strongest single predictor of decomposition rate for leaves. Although temperatures are relatively warm and constant in the tropics, precipitation regimes and amounts vary widely. The strong correlation of decomposition with CDI likely reflects the importance of

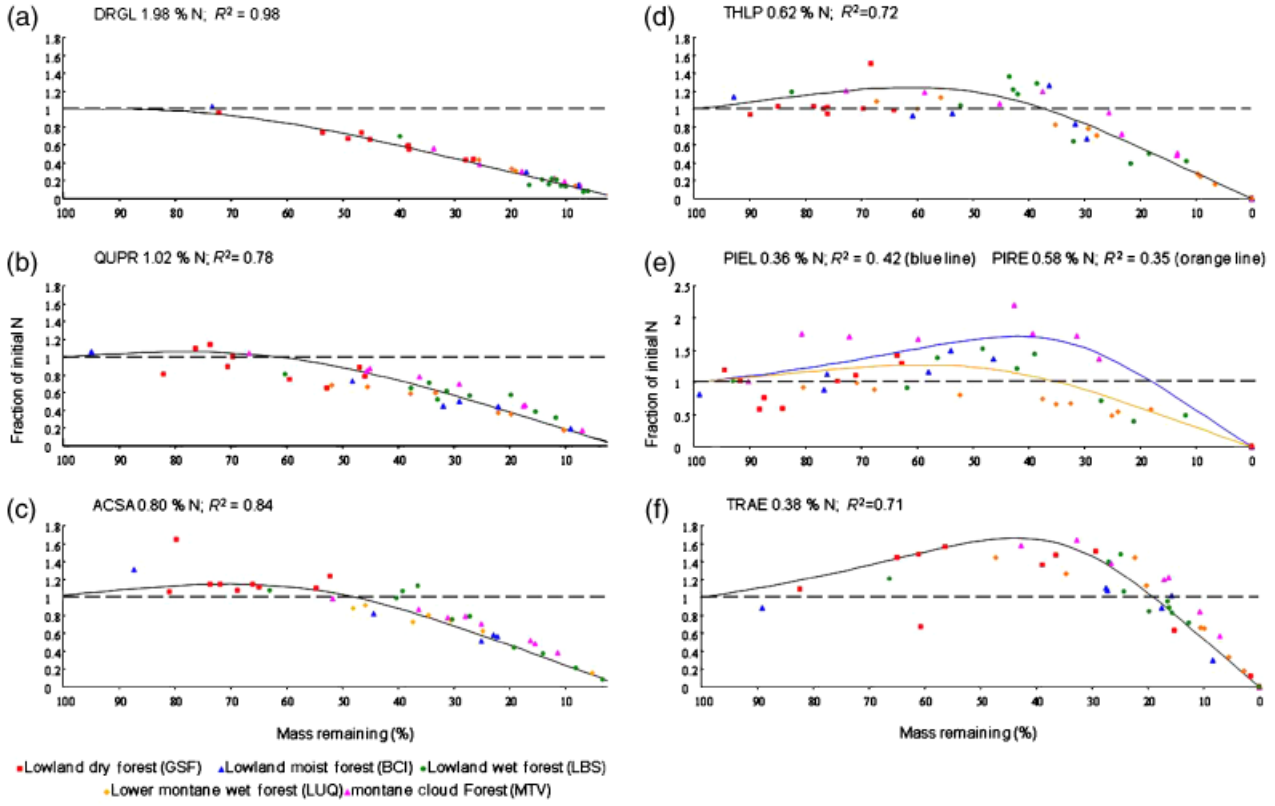

Fig. 3 Nitrogen immobilization and release across sites for leaf litter species (a) DRGL, (b) QUPR, (c) ACSA, (d) THLP, (e) PIEL (blue line) and PIRE (orange line), and (f) TRAE. Initial litter N concentration is indicated for each species. The horizontal line at 1 represents 100% of initial N concentrations. Data above the line represent N immobilization, and data below the line represent N release.

seasonality in precipitation for decomposition rates. For leaf litters, all precipitation-related climate parameters (MAP, CDI, and AET) were more strongly correlated with time to 50% mass remaining than with long-term time-integrated *k*-values. This result is similar to findings from analyses of the global LIDET dataset (Currie *et al*., in review), where climate parameters were strong predictors of early phases of decomposition but not of long-term integrated decomposition. The dependence of early-phase decomposition on precipitation and related climate indices in tropical forests likely reflects the importance of leaching of soluble compounds (Cleveland *et al*., 2004). The significant positive correlation of MAT with time to 50% mass remaining for root litter is surprising and may indicate a high degree of sensitivity of tropical soil microbes to even small changes in temperature (Silver, 1998).

We expected to see the most rapid decomposition rates at the wettest, warmest lowland forest site, LBS. However, BCI and LUQ, both of which had lower MAP, had faster long-term leaf and root decomposition rates than LBS (Table 1). Two other studies at LBS found substantially faster 1-year decomposition rates for native litters (Kershnar & Montagnini, 1998; Horn & Montagnini, 1999). However, the longer period of decomposition of the LIDET experiment (4.4 years at LBS) likely captured an important dynamic of slow-pool C decomposition not observed in shorter studies with native litters. LBS had the fastest rates of initial decomposition (time to 50% mass remaining), indicating that the gamma radiation did not inhibit early mass loss at this site. Despite rapid early decomposition, the long slow phase of decomposition gave LBS the lower integrated *k*-value relative to BCI and LUQ.

The slowest leaf and root litter decomposition was at GSF, probably related to severe drought during part of the year. Root decomposition was also slow at MTV. Lower temperatures combined with soil saturation and low oxygen diffusion under high precipitation in the cloud forest (MTV) may have inhibited decomposer organisms (Bloomfield *et al*., 1993; McGroddy & Silver, 2000; Schuur, 2001).

Litter chemistry controls on decomposition in tropical forests

Key chemical controls for leaf and root decomposition were similar and included the initial concentrations of

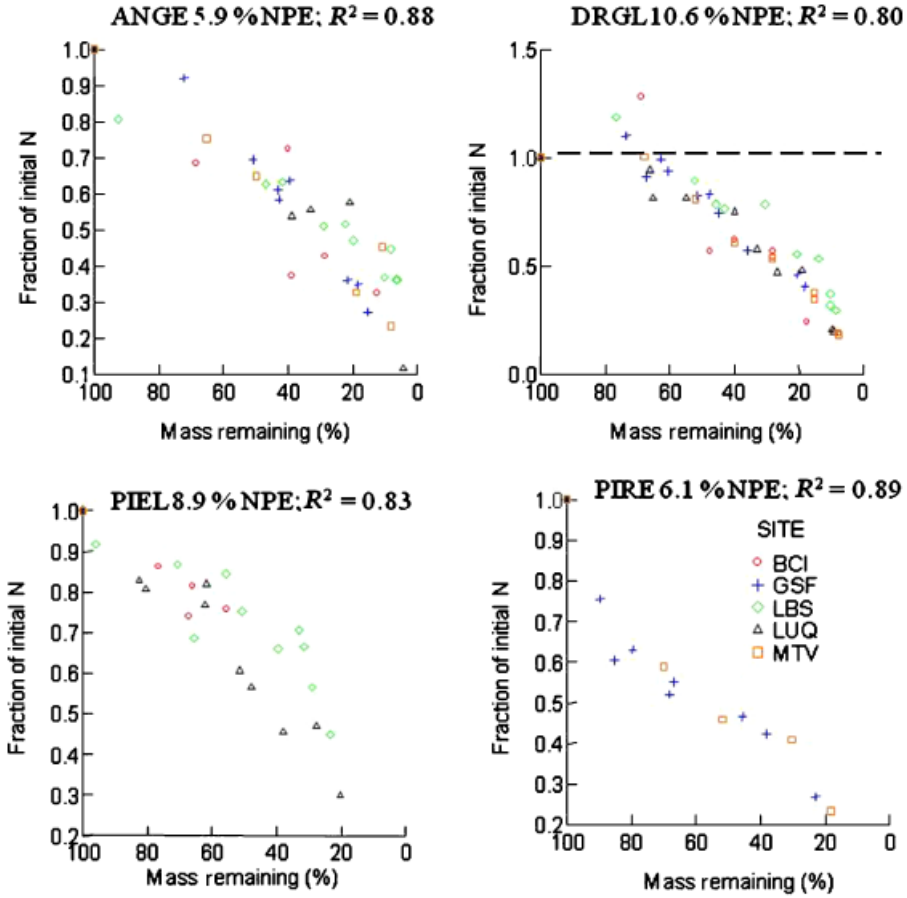

Fig. 4 Nitrogen immobilization and release across sites for root litter species (a) ANGE, (b) DRGL, (c) PIEL, and (d) PIRE. The initial concentration of nonpolar extractives (NPE) in root litter is indicated for each species. The horizontal line at 1 represents 100% of initial N, and is shown only for species with N immobilization. Data above the line represent N immobilization, and data below the line represent N release.

lignin, N and nonpolar extractives. Leaf litter of the fastest decomposing species (DRGL) had the highest initial N concentrations and the lowest lignin : N in the dataset, while the most slowly decomposing leaf litter (PIEL) had the highest lignin : N. The importance of litter N concentrations for decomposer activity has been reported for other tropical forests, particularly in montane environments (Silver, 1998; Hobbie & Vitousek, 2000). Other nutrients not measured here, including phosphorous and micronutrients, have also been shown to play an important role in tropical decomposition (Cleveland *et al*., 2006; Kaspari *et al*., 2008), though the strong correlations found here indicate that climate, N, and C chemistry of tissues may provide dominant controls on tropical decomposition.

The root species with the slowest decomposition rates (PIEL and PIRE) had the highest lignin concentrations (Table 3), and lignin was the single best predictor of root decomposition across the three sites that included PIEL roots. Factors combining lignin and N have traditionally been used to predict long-term decomposition patterns across biomes, where N concentrations have been found to be more important during early decomposition, and lignin more important during later stages (Tripathi & Singh, 1992; Berg & Matzner, 1997). Lignin may be especially important in moist tropical and humid forests; high rainfall encourages rapid initial decomposition, leading to higher relative lignin concentrations in later stages of decomposition (Couteaux *et al*., 1995). This interaction between precipitation and lignin could help explain the slower long-term decomposition at the wettest site (LBS), as well as the slower decomposition of the high lignin litters.

Nonpolar extractives, composed primarily of fats, oils, and waxes, were also good predictors of both leaf and root decomposition rates. Short-term tropical forest decomposition studies (1 year or less) generally have not found significant relationships between nonpolar

Table 5 Predictors of nitrogen release from root litter†

Factor(s)	Root R^2
M_R	0.64
M_R + MAP	0.66
M_R + MAT	0.65*
M_R + AET	0.67
M_R + CDI	0.66
M_R + %N	0.72
M_R + C : N	**0.79**
M_R + lignin : N	ns
M_R + lignin	0.66
M_R + NPE	0.72
M_R + tannins	ns
M_R + WSC	0.72
M_R + ASC	ns
M_R + % N + NPE	0.79
M_R + % N + WSC	0.75

†Regressions of root N remaining vs. climate and chemical parameters are shown (all concentrations are in %). Percent N remaining is of initial N for each tissue type; data from all species at all sites are included. Fraction of ash-free mass remaining (M_R) was included as the main explanatory factor in all regressions. The simplest model with the best fit is shown in bold and has the following equation, where N_f is fraction of N remaining in root tissue and $C:N_i$ is initial tissue C : N:

$N_f = 0.01 \times M_R - 0.01 \times C:N_i - 0.5$.

*$P < 0.1$ for one factor. For all other factors and for regressions overall, $P < 0.05$.

extractives and mass loss (Smith *et al*., 1998; Ostertag & Hobbie, 1999). The leaf litters with the highest concentrations of nonpolar extractives, PIEL, PIRE, and THLP (all coniferous species), had the slowest decomposition rates (Table 3). Nonpolar extractives tend to be relatively insoluble, providing a control on decomposition rates in wetter sites.

Leaf vs. root decomposition

We found no difference between average leaf and root decomposition rates for the five tropical forests included here. Our results contrast with Gholz *et al*. (2000), who found that the ratio of above- to belowground decomposition varied greatly among sites in the temperate zone. Currie *et al*. (in review) also found that long-term root litter decomposition was slower than leaf decomposition across all the LIDET sites. Previous work has suggested that, at regional or global scales, aboveground decomposition may be more sensitive to climate (Meentemeyer, 1978a), whereas root decomposition may depend more heavily on tissue chemistry (Silver & Miya, 2001). Root and leaf litter from the same plant species often decompose at different rates across biomes, with roots generally decomposing more slowly (Bloomfield *et al*., 1993; Bryant *et al*., 1998; Gorissen & Cotrufo, 2000; Kemp *et al*., 2003; Majdi, 2004), likely related to litter chemical characteristics (Bloomfield *et al*., 1993). Roots typically have higher lignin and C : N than leaves (Galletti *et al*., 1993; Moretto *et al*., 2001; Moretto & Distel, 2003; Abiven *et al*., 2005). Thus, litter chemistry is often a confounding factor when comparing leaf and root decomposition. In this study, there were very few significant differences in average root vs. leaf litter chemistry across species (although phosphorous, which is likely to be important in tropical forest nutrient dynamics, was not measured). The similarity of root and leaf decomposition rates in these tropical forests is likely related to similarity in tissue chemistry, with more favorable microclimatic conditions belowground than in temperate systems (Borneman & Triplett, 1997). We did find important differences in both climate and tissue chemistry drivers of root vs. leaf decomposition. Rainfall seasonality (CDI) most strongly drove leaf decomposition, while temperature and lignin concentrations drove root decomposition.

Litter nitrogen dynamics

We observed different patterns of N release from leaf vs. root litter across the five tropical forest types, and patterns observed here were generally consistent with global trends (Parton *et al*., 2007). We expected that the initial N concentration would be a strong predictor of N release from both leaf litter (Frankenberger & Abdelmagid, 1985; Constantinides & Fownes, 1994; Arunachalam *et al*., 2005) and root litter (Chen *et al*., 2002). Leaf litter species with N $\leq 1\%$ showed initial net N immobilization followed by net N mineralization, with all species exhibiting nonlinear patterns of N release (Fig. 3). These results are consistent with patterns found in seven litter species decomposed in a Japanese subtropical forest (Xu & Hirata, 2005). Previous studies suggest that the breakpoint between net immobilization and net mineralization is 1.8–2.5% N (Palm *et al*., 2001) or a C : N of 27 (Seneviratne, 2000), with N immobilization occurring at lower initial N concentrations and higher C : N. Accordingly, the only leaf litter in our study that showed no net N immobilization (DRGL) had an initial N concentration of 2.0% and a C : N of 24.

All root litter species had low initial N and high C : N relative to the net immobilization breakpoint, suggesting that N immobilization would be observed during decomposition. However, relatively linear patterns in N release were observed for all root litter species. This is consistent with recent work showing that roots across all LIDET sites released N linearly with mass loss, regardless of species or location (Parton *et al*., 2007). In

Table 6 Decomposition rate constants for native species studies in tropical Long-Term Intersite Decomposition Experiment (LIDET) sites and Hawaii

Study	Site	Species	Length of study (year)	*k*-value (mean ± SE)
Cornejo *et al*. (1994)*	BCI	*Anacardium*, *Hyeronima*, *Prioria*, *Quararibea*, *Tetragastris*	0.5	0.61 ± 0.11
Wieder & Wright (1995)†	BCI	Unidentified native species	5	1.65 ± 0.04
Lugo & Murphy (1986)	GSF	Unidentified native species	2.1	0.413
Kershnar & Montagnini (1998)*	LBS	Mixed native species	1	2.4
Horn & Montagnini (1999)*	LBS	Mixed native species	1	3.8
Bloomfield *et al*. (1993)	LUQ	*Dacroydes excelsa*	1	1.6
Bloomfield *et al*. (1993)	LUQ	*Prestoea montana*	1	1.3
Ruan *et al*. (2005)	LUQ	6 + native species	1	1.30 ± 0.08
Dechaine *et al*. (2005)	LUQ	6 + native species	1	1.47
Shiels (2006)	LUQ	*Cyathea* (tree fern)	1	0.93 ± 0.06
Shiels (2006)	LUQ	*Cecropia*	1	0.68 ± 0.06
Nadkarni & Matelson (1992)†,‡	MTV	Unidentified native species	3	0.69
Clark *et al*. (1998)	MTV	Native bryophyte	1.25	0.56
Austin & Vitousek (2000)§	Hawaii	*Metrosideros polymorpha* (dry-site litter)	2	0.16–0.06
Austin & Vitousek (2000)§	Hawaii	*Metrosideros polymorpha* (wet-site litter)	2	0.22–2.06
Schuur (2001)	Hawaii	*Metrosideros polymorpha*	1.25	0.35–1.48

**k*-values were not reported, available mass loss data were used in a single exponential decay model to calculate *k*-values.
†Decomposition rate determined by mass balance.
‡Leaves, roots, and twigs decomposed.
§Litter was decomposed over a rainfall gradient spanning five sites: 500, 900, 1500, 2200, 5000 mm. Dry-site litter was collected at the 500 mm site, and wet-site litter was collected at the 5000 mm site; both litter types were decomposed across the Hawaiian precipitation gradient for this study.

our study, initial N was not a reliable indicator of net N immobilization in root tissues; mass loss was the best predictor of net N release, suggesting that N was less limiting to decomposition of root tissues compared with foliar tissues. We observed short-term net immobilization only for DRGL roots, the single tropical species in the study. DRGL did not have the lowest initial N concentration among root species but did have the highest C : N. Notably, DRGL root litter also had the highest initial concentration of nonpolar extractives, which we identified as one of the best predictors of net N release from root tissues. Nonpolar extractives have not previously been linked to net N release patterns, but our data suggest that they may be directly or indirectly related to N release from roots in tropical sites.

We observed some site-level differences in leaf litter N dynamics. Montane tropical forests are often assumed to be N-limited (Tanner *et al*., 1998), and one might expect to see higher net N immobilization at these sites. Although MTV, a montane cloud forest, had higher rates of net N immobilization than some of the lower elevation sites, we also found considerable net N immobilization in the lowland dry forest (GSF, Fig. 4). The lower elevation tropical forests with the most rapid decomposition rates (LUQ and BCI) had the lowest net N immobilization.

Comparisons with native species litter decomposition studies

Decomposition rates reported here were generally similar to compiled data on decomposition rates of native species at the same sites, with the exception of LBS. Our regressions of MAP and MAT vs. leaf *k*-values for the compiled dataset showed a positive relationship between decomposition and MAP across litter species to 5500 mm MAP (Fig. 5). The relationship we found between leaf litter decomposition and precipitation is consistent with a 2-year study along a 500–5500 mm precipitation gradient in Hawaiian tropical forests (Austin & Vitousek, 2000), but contrasts with another precipitation-gradient study in Hawaii, which reported an inverse relationship between decomposition and precipitation, presumably due to the prevalence of anoxic conditions in wetter soils (Schuur, 2001). Site effects on decomposition could be related to factors other than climate and substrate quality, such as the

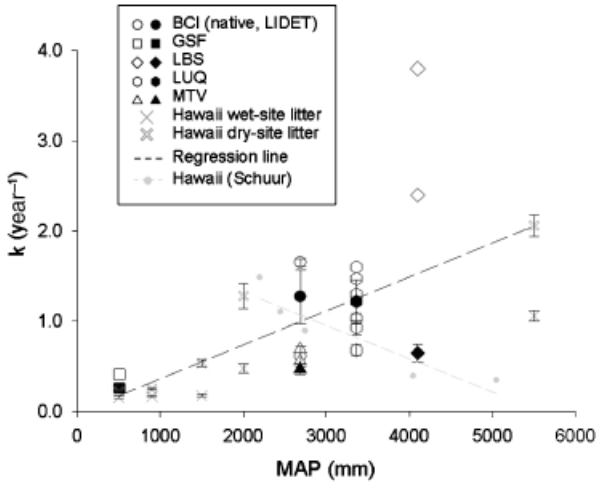

Fig. 5 Decomposition rate constants (k) vs. mean annual precipitation (MAP). Closed symbols represent leaf decomposition data for the Long-Term Intersite Decomposition Experiment (LIDET) standard substrates at five LIDET tropical forest sites. Open symbols represent data from other published studies of native species decomposition at the same sites (Table 6). Crosses represent data reported by Austin & Vitousek (2000) for native species decomposed on a precipitation gradient on Hawaii; litter for the Hawaii experiment was transplanted, and dry and wet refer to the site conditions where the litter was collected. Light gray symbols and regression line show a contrasting trend found along a different Hawaiian precipitation gradient (Schuur, 2001). The equation of the dark regression line (excluding Schuur, 2001) is: $k = -0.011 + 0.0004 \times \text{MAP}$, with $R^2 = 0.43$, $P < 0.05$.

composition and activity of local soil fauna (Heneghan *et al*., 1999; Alhamd *et al*., 2004), or other unmeasured edaphic conditions (Scowcroft *et al*., 2000). Our results imply that the LIDET dataset was generally representative of native species decomposition in tropical forests, including the potential for very high rainfall to suppress decomposition of specific litters at individual sites (Appendix A).

Conclusions

Our results have important implications for predicting rates of C and nutrient cycling in tropical forest biomes in a changing world. We found strong correlations between climate and decomposition rates in neotropical forests, especially during early stages of decomposition. Our results add to the growing evidence that tropical forest biogeochemical cycles are sensitive to even small changes in climate. Tropical forests account for a significant proportion of global C pools and fluxes, and in future decades, these environments are projected to experience warming, precipitation changes, and increasing anthropogenic N deposition, all of which are likely to alter rates of C and nutrient cycling. Understanding the relative importance of climatic and chemical controls on decomposition rates improves our ability to predict ecosystem responses to global change.

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References

Aber JD, Melillo JM (1980) Litter decomposition – measuring relative contributions of organic matter and nitrogen to forest soils. *Canadian Journal of Botany*, **58**, 416–421.

Abiven S, Recous S, Reyes V, Oliver R (2005) Mineralisation of C and N from root, stem and leaf residues in soil and role of their biochemical quality. *Biology and Fertility of Soils*, **42**, 119–128.

Adair EC, Parton WJ, Del Grosso SJ, Silver WL, Hall SA, Harmon ME, Hart SC (2008) A simple three pool model accurately describes patterns of long term, global decomposition in the Long-Term Intersite Decomposition Experiment Team (LIDET) data set. *Global Change Biology*, **14**, 2636–2660.

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, **79**, 439–449.

Alhamd L, Arakaki S, Hagihara A (2004) Decomposition of leaf litter of four tree species in a subtropical evergreen broad-leaved forest, Okinawa Island, Japan. *Forest Ecology and Management*, **202**, 1–11.

Arunachalam A, Singh ND (2004) Decomposition of *Mesua ferrea* litter in humid tropics of Arunachal Pradesh, India. *Journal of Tropical Forest Science*, **16**, 151–159.

Arunachalam A, Upadhyaya K, Arunachalam K, Pandey HN (2005) Litter decomposition and nutrient mineralization dynamics in two bamboo species growing in a 9-year-old ''jhum'' fallow. *Journal of Tropical Forest Science*, **17**, 33–44.

Austin AT, Vitousek PM (2000) Precipitation, decomposition and litter decomposability of *Metrosideros polymorpha* in native forests on Hawai'i. *Journal of Ecology*, **88**, 129–138.

Berg B, Matzner E (1997) Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. *Environmental Reviews*, **5**, 1–25.

Bills GF, Polishook JD (1994) Abundance and diversity of microfungi in leaf litter of a lowland rain forest in Costa Rica. *Mycologia*, **86**, 187–198.

Bloomfield J, Vogt KA, Vogt DJ (1993) Decay rate and substrate quality of fine roots and foliage of 2 tropical tree species in the Luquillo Experimental Forest, Puerto Rico. *Plant and Soil*, **150**, 233–245.

Borneman J, Triplett EW (1997) Molecular microbial diversity in soils from eastern Amazonia: evidence for unusual microorganisms and microbial population shifts associated with deforestation. *Applied and Environmental Microbiology*, **63**, 2647–2653.

Bryant DM, Holland EA, Seastedt TR, Walker MD (1998) Analysis of litter decomposition in an alpine tundra. *Canadian Journal of Botany*, **76**, 1295–1304.

Carney KM, Matson PA (2005) Plant communities, soil microorganisms, and soil carbon cycling: does altering the world belowground matter to ecosystem functioning? *Ecosystems*, **8**, 928–940.

Chen H, Harmon ME, Griffiths RP (2001) Decomposition and nitrogen release from decomposing woody roots in coniferous forests of the Pacific Northwest: a chronosequence approach. *Canadian Journal of Forest Research*, **31**, 246–260.

Chen H, Harmon ME, Sexton J, Fasth B (2002) Fine root decomposition and nitrogen dynamics in coniferous forests of the Pacific Northwest, USA. *Canadian Journal of Forest Research*, **32**, 320–331.

Clark DL, Nadkarni NM, Gholz HL (1998) Growth, net production, litter decomposition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest. *Biotropica*, **30**, 12–23.

Cleveland CC, Neff JC, Townsend AR, Hood E (2004) Composition, dynamics, and fate of leached dissolved organic matter in terrestrial ecosystems: results from a decomposition experiment. *Ecosystems*, **7**, 275–285.

Cleveland CC, Reed SC, Townsend AR (2006) Nutrient regulation of organic matter decomposition in a tropical rain forest. *Ecology*, **87**, 492–503.

Constantinides M, Fownes JH (1994) Nitrogen mineralization from leaves and litter of tropical plants – relationship to nitrogen, lignin and soluble polyphenol concentrations. *Soil Biology and Biochemistry*, **26**, 49–55.

Cornejo FH, Varela A, Wright SJ (1994) Tropical forest litter decomposition under seasonal drought – nutrient release, fungi and bacteria. *Oikos*, **70**, 183–190.

Couteaux MM, Bottner P, Berg B (1995) Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution*, **10**, 63–66.

Cuevas E, Medina E (1988) Nutrient dynamics within Amazonian forests. 2. Fine root growth, nutrient availability and leaf litter decomposition. *Oecologia*, **76**, 222–235.

Currie WS, Harmon ME, Burke I, Hart SC, Parton WJ, Silver WL (in review) Extension and limitation of the climate-litter quality paradigm to predict controls on plant litter decomposition over a decade. *Global Change Biology*.

Dechaine J, Ruan HH, Leon YSD, Zou XM (2005) Correlation between earthworms and plant litter decomposition in a tropical wet forest of Puerto Rico. *Pedobiologia*, **49**, 601–607.

Frankenberger WT, Abdelmagid HM (1985) Kinetic parameters of nitrogen mineralization rates of leguminous crops incorporated into soil. *Plant and Soil*, **87**, 257–271.

Galletti GC, Reeves JB, Bloomfield J, Vogt KA, Vogt DJ (1993) Analysis of leaf and fine-root litter from a subtropical montane rain forest by pyrolysis-gas chromatography mass spectrometry. *Journal of Analytical and Applied Pyrolysis*, **27**, 1–14.

Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology*, **6**, 751–765.

Goma-Tchimbakala J, Bernhard-Reversat F (2006) Comparison of litter dynamics in three plantations of an indigenous timber-tree species (*Terminalia superba*) and a natural tropical forest in Mayombe, Congo. *Forest Ecology and Management*, **229**, 304–313.

Gonzalez G, Seastedt TR (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology*, **82**, 955–964.

Gorissen A, Cotrufo MF (2000) Decomposition of leaf and root tissue of three perennial grass species grown at two levels of atmospheric CO_2 and N supply. *Plant and Soil*, **224**, 75–84.

Gosz JR, Likens GE, Bormann FH (1973) Nutrient release from decomposing leaf and branch litter in Hubbard Brook Forest, New Hampshire. *Ecological Monographs*, **43**, 173–191.

Goulden ML, Miller SD, da Rocha HR, Menton MC, de Freitas HC, Figueira A, de Sousa CAD (2004) Diel and seasonal patterns of tropical forest CO_2 exchange. *Ecological Applications*, **14**, S42–S54.

Harmon ME, Baker GA, Spycher G, Greene SE (1990) Leaf litter decomposition in the *Picea tsuga* forests of Olympic National Park, Washington, USA. *Forest Ecology and Management*, **31**, 55–66.

Heneghan L, Coleman DC, Zou X, Crossley DA, Haines BL (1999) Soil microarthropod contributions to decomposition dynamics: tropical-temperate comparisons of a single substrate. *Ecology*, **80**, 1873–1882.

Hobbie SE, Vitousek PM (2000) Nutrient limitation of decomposition in Hawaiian forests. *Ecology*, **81**, 1867–1877.

Holdridge LR, Grenke WC, Hatheway WH, Liang T, Tosi JA (1971) *Forest Environments in Tropical Life Zones: A Pilot Study.* Pergamon Press, New York, NY.

Horn N, Montagnini F (1999) Litterfall, litter decomposition and maize bioassay of mulches from four indigenous tree species in mixed and monospecific plantations in Costa, Rica. *International Tree Crops Journal*, **10**, 37–50.

Kaspari M, Garcia MN, Harms KE, Santana M, Wright SJ, Yavitt JB (2008) Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecology Letters*, **11**, 35–43.

Kemp PR, Reynolds JF, Virginia RA, Whitford WG (2003) Decomposition of leaf and root litter of Chihuahuan desert shrubs: effects of three years of summer drought. *Journal of Arid Environments*, **53**, 21–39.

Kershnar R, Montagnini F (1998) Leaf litter decomposition, litterfall, and effects of leaf mulches from mixed and monospecific plantations in Costa Rica. *Journal of Sustainable Forestry*, **7**, 95–118.

LIDET (1995) *Meeting the Challenges of Long-Term, Broad-Scale Ecological Experiments, Publication. No. 19.* U.S. LTER Network Office, Seattle, WA.

Loranger G, Ponge JF, Imbert D, Lavelle P (2002) Leaf decomposition in two semi-evergreen tropical forests: influence of litter quality. *Biology and Fertility of Soils*, **35**, 247–252.

Lugo A, Murphy P (1986) Nutrient dynamics of a Puerto Rican subtropical dry forest. *Journal of Tropical Ecology*, **2**, 55–76.

Majdi H (2004) Root and needle litter decomposition responses to enhanced supplies of N and S in a Norway spruce forest in southwest Sweden. *Plant Biosystems*, **138**, 225–230.

McClaugherty C, Berg B (1987) Cellulose, lignin, and nitrogen concentrations as rate regulating factors in late stages of forest litter decomposition. *Pedobiologia*, **30**, 101–112.

McGroddy M, Silver WL (2000) Variations in belowground carbon storage and soil CO_2 flux rates along a wet tropical climate gradient. *Biotropica*, **32**, 614–624.

Meentemeyer V (1978a) Macroclimate and lignin control of litter decomposition rates. *Ecology*, **59**, 465–472.

Meentemeyer V (1978b) An approach to the biometeorology of decomposer organisms. *International Journal of Biometeorology*, **22**, 94–102.

Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, **63**, 621–626.

Melillo JM, Mcguire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. *Nature*, **363**, 234–240.

Moretto AS, Distel RA (2003) Decomposition of and nutrient dynamics in leaf litter and roots of *Poa ligularis* and *Stipa gyneriodes*. *Journal of Arid Environments*, **55**, 503–514.

Moretto AS, Distel RA, Didone NG (2001) Decomposition and nutrient dynamic of leaf litter and roots from palatable and unpalatable grasses in a semi-arid grassland. *Applied Soil Ecology*, **18**, 31–37.

Nadkarni NM, Matelson TJ (1992) Biomass and nutrient dynamics of fine litter of terrestrially rooted material in a neotropical montane forest, Costa Rica. *Biotropica*, **24**, 113–120.

Olson JS (1963) Energy storage and balance of producers and decomposers in ecological systems. *Ecology*, **44**, 322–331.

Ostertag R, Hobbie SE (1999) Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. *Oecologia*, **121**, 564–573.

Palm C, Gachengo C, Delve R, Cadisch G, Giller K (2001) Organic inputs for soil fertility management in tropical agroecosystems: application of an organic residue database. *Agriculture, Ecosystems and Environment*, **83**, 27–42.

Parton* W, Silver* WL, Burke I *et al*. (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science*, **315**, 361–364. *Co-lead authors.

Parton WJ, Schimel DS, Ojima DS, Cole CV (1994) A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. In: *Quantitative Modeling of Soil Forming Processes* (eds Bryant RB, Arnold RW), pp. 147–167. SSSA Special Publication 39. ASA, CSSA, SSA, Madison, WI.

Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus Series B – Chemical and Physical Meteorology*, **44**, 81–99.

Ruan HH, Li YQ, Zou XM (2005) Soil communities and plant litter decomposition as influenced by forest debris: variation across tropical riparian and upland sites. *Pedobiologia*, **49**, 529–538.

Ryan MG, Melillo JM, Ricca A (1990) A comparison of methods for determining proximate carbon fractions of forest litter. *Canadian Journal of Forest Research*, **20**, 166–171.

Sanchez PA (1976) *Properties and Management of Soils in the Tropics*. Wiley, New York.

Schlesinger WH, Andrews JA (2000) Soil respiration and the global carbon cycle. *Biogeochemistry*, **48**, 7–20.

Schuur EAG (2001) The effect of water on decomposition dynamics in mesic to wet Hawaiian montane forests. *Ecosystems*, **4**, 259–273.

Scott NA, Binkley D (1997) Foliage litter quality and annual net N mineralization: comparison across North American forest sites. *Oecologia*, **111**, 151–159.

Scowcroft PG, Turner DR, Vitousek PM (2000) Decomposition of *Metrosideros polymorpha* leaf litter along elevational gradients in Hawaii. *Global Change Biology*, **6**, 73–85.

Seneviratne G (2000) Litter quality and nitrogen release in tropical agriculture: a synthesis. *Biology and Fertility of Soils*, **31**, 60–64.

Shiels AB (2006) Leaf litter decomposition and substrate chemistry of early successional species on landslides in Puerto Rico. *Biotropica*, **38**, 348–353.

Silver WL (1998) The potential effects of elevated CO_2 and climate change on tropical forest soils and biogeochemical cycling. *Climatic Change*, **39**, 337–361.

Silver WL, Miya RK (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia*, **129**, 407–419.

Smith CK, Gholz HL, Oliveira FD (1998) Fine litter chemistry, early-stage decay, and nitrogen dynamics under plantations and primary forest in Lowland Amazonia. *Soil Biology and Biochemistry*, **30**, 2159–2169.

Tanner EVJ, Vitousek PM, Cuevas E (1998) Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology*, **79**, 10–22.

Tiwari SC, Tiwari BK, Mishra RR (1994) Succession of microfungi associated with the decomposing litters of pineapple (*Ananas comosus*). *Pedobiologia*, **38**, 185–192.

Tripathi SK, Singh KP (1992) Abiotic and litter quality control during the decomposition of different plant parts in dry tropical bamboo savanna in India. *Pedobiologia*, **36**, 241–256.

Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, **65**, 285–298.

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea – how can it occur. *Biogeochemistry*, **13**, 87–115.

Wieder RK, Wright SJ (1995) Tropical forest litter dynamics and dry season irrigation on Barro Colorado Island, Panama. *Ecology*, **76**, 1971–1979.

Wood TG (1974) Field investigations on decomposition of leaves of *Eucalyptus delegatensis* in relation to environmental factors. *Pedobiologia*, **14**, 343–371.

Xu XN, Hirata EJ (2005) Decomposition patterns of leaf litter of seven common canopy species in a subtropical forest: N and P dynamics. *Plant and Soil*, **273**, 279–289.

Appendix A

Table A1 Long-term time-integrated *k*-values (year^{-1}) for LIDET species* across sites and tissue types

Tissue type	Species	BCI	GSF	LBS	LUQ	MTV
Leaf	ACSA	1.28†	0.18	0.77	1.15	0.47
	DRGL	2.54†	0.40	1.08	2.17	0.67
	PIEL	0.45†	0.13	na	na	na
	PIRE	na	na	0.43	0.65	0.23
	QUPR	1.23†	0.25†	0.50	0.67†	0.44†
	THPL	0.71	0.12	0.49	1.06†	0.40
	TRAE	1.43	0.50†	0.65	1.61	0.61
Root	ANGE	1.14	0.54	0.82	1.57	0.62
	DRGL	1.00	0.42	0.69	1.01†	0.52
	PIEL	0.30	na	0.36	0.59†	na
	PIRE	na	0.31†	na	na	0.35†

*Only one *Pinus* species was decomposed at each site for leaves and roots.

†Denotes combinations of site, species, and litter type for which *k*-values were calculated using a single-phase time-integrated decomposition model. All other combinations were best described using a two-phase model.

