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Litter Decomposition Within the Canopy and Forest Floor of Three Tree Species in a Tropical Lowland Rain forest, Costa Rica

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ABSTRACT

The rain forest canopy hosts a large percentage of the world's plant biodiversity, which is maintained, in large part, by internal nutrient cycling. This is the first study to examine the effects of site (canopy, forest floor) and tree species (*Dipteryx panamensis*, *Lecythis ampla*, *Hyeronima alchorneoides*) on decay rates of a common substrate and *in situ* leaf litter in a tropical forest in Costa Rica. Decay rates were slower for both substrates within the canopy than on the forest floor. The slower rate of mass loss of the common substrate in the canopy was due to differences in microclimate between sites. Canopy litter decay rates were negatively correlated with litter lignin: P ratios, while forest floor decay rates were negatively correlated with lignin concentrations, indicating that the control of litter decay rates in the canopy is P availability while that of the forest floor is carbon quality. The slower cycling rates within the canopy are consistent with lower foliar nutrient concentrations of epiphytes compared with forest floor-rooted plants. Litter decay rates, but not common substrate decay rates, varied among tree species. The lack of variation in common substrate decay among tree species eliminated microclimatic variation as a possible cause for differences in litter decay and points to variation in litter quality, nutrient availability and decomposer community of tree species as the causal factors. The host tree contribution to canopy nutrient cycling via litter quality and inputs may influence the quality and quantity of canopy soil resources.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: La Selva; lignin:P; litter quality; nutrient cycling.

DECOMPOSITION IS A FUNDAMENTAL ECOSYSTEM PROCESS that exerts substantial controls over nutrient cycling by mineralizing nutrients bound in organic forms (Swift *et al.* 1979). In tropical systems, decomposition on the forest floor may be supplemented by litter accumulation and decomposition within the canopy. The canopy is a significant and important habitat within tropical forests because it hosts up to 35 percent of the vascular flora (Gentry & Dodson 1987, Nieder *et al.* 2001), a richness complementary to that on the forest floor (Cardelús 2002, Watkins *et al.* 2006), and a large proportion of the invertebrate biomass and diversity (Erwin 1997, Ellwood & Foster 2004, Dial *et al.* 2006). This high diversity within the canopy is supported by nutrients coming from both internal and external nutrient sources. Internal sources include nutrient cycling via canopy soil, an arboreal histosol putatively derived from epiphyte and host tree litter (Nadkarni 1986, Stewart *et al.* 1995, Hietz *et al.* 1999) and throughfall. External sources of nutrients include deposition and precipitation (Nadkarni 1986, Stewart *et al.* 1995, Hietz *et al.* 1999). The most nutrient-rich N source within the canopy is canopy soil (Nadkarni 1986, Stewart *et al.* 1995, Hietz *et al.* 1999). Both soil bulk N concentrations, C:N ratios and N:P ratios are significantly higher in canopy compared with forest floor mineral soils (A horizon) (Vance & Nadkarni 1990, Nadkarni *et al.* 2004, Cardelús *et al.* 2009). These high C:N and N:P ratios may stimulate immobilization of N and P in microbial biomass, thereby limiting N and P availability to plants. Consistent with this notion are the significantly lower foliar N concentrations in epiphytes compared with forest floor rooted plants (Hofstede *et al.* 1993, Hietz *et al.* 2002, Watkins *et al.* 2007).

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The host tree defines the canopy's habitat as it provides the substrate for establishment and modulates microclimate through tree architecture and phenology (Pittendrigh 1948, Hietz & Briones 1998, Cardelús & Chazdon 2005, Cardelús & Watkins in press). Tree species may influence canopy nutrient cycling indirectly via microclimate—which is influenced by tree architecture and phenology. This can have direct effects on canopy soil through moisture and temperature regulation of microbial decomposition (Pittendrigh 1948, Hietz & Briones 1998, 2001, Cardelús & Chazdon 2005, Cardelús & Watkins in press). In some studies, species-driven effects have been found to directly and/or indirectly affect their forest floor soil environment (Zinke 1962, Prescott 2002) while in others they have been found to have no effect (Powers *et al.* 2004).

Host trees may also influence nutrient cycling via host tree litter quality. It is unclear whether leaf litter from one particular host tree remains in the canopy of that host tree during the majority of its decomposition period. In the single known study of leaf attrition and decomposition in the canopy, which was conducted in a lower montane forest in Costa Rica, Nadkarni and Matelson (1991) found that 70 percent of litter was lost from the canopy within two weeks of leaffall, likely due to high wind speeds that often exceeded 100 km/hr during storms. Together, this evidence indicates that leaf litter can be removed from the canopy before entering canopy soil. However, litter may remain within the canopy longer in lowland rain forests where wind speeds are lower, or in 'protected' microsites within the canopy. In these forests, maximum wind speeds reach only *ca* 4.5–11.5 km/h in Costa Rica (this study site, La Selva Biological Station) and Brazil, respectively (Kruijt *et al.* 2000, McCay 2003). As a result, the litter chemistry of host trees may be more likely to influence the composition of canopy soils in tropical lowland forests than in montane forests.

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This is the first study to examine litter decay rates both between the canopy and on the forest floor and among tree species in a lowland tropical rain forest. I have used both a common substrate and an *in situ* litter experiment within the canopy and forest floor environment of three tree species with different life histories to distinguish the effects of microclimate from host tree effects. I predicted that decay rates would be slower within the canopy compared with the forest floor because of the lower humidity (J. E. Watkins, Jr., unpubl. data; Cardelús & Chazdon 2005) and the frequent and rapid drying events within the canopy that dry out the entire epiphyte mat and associated soil (Coxson *et al*. 1992, Bohlman *et al*. 1995, Coxson & Nadkarni 1995). I also predicted I would find differences in decay rates among tree species due to variation in litter quality and microclimate due, in large part, to differences in phenology.

METHODS

STUDY SITE.—This study was conducted at the La Selva Biological Station in Northeastern Costa Rica (10°25′52N, 84°00′12W; 40 m asl). La Selva is a 1500 ha predominantly old growth tropical wet forest which receives *ca* 4000 mm of rainfall per year with a moderate dry season during March–April (McDade *et al*. 1994). Diurnal temperature fluctuation (19–31°C) is greater than seasonal variation (24.7–27.1°C). The lack of variability in relative humidity, air temperature, and solar radiation at La Selva are notable features of the site's climate (Sanford *et al*. 1994). Elevational range at the site is 20–130 m. Percent light transmittance in the forest floor is *ca* 1–2 percent (Chazdon & Fetcher 1984) compared with the canopy which is 6–23 percent depending on the tree species (Cardelús & Chazdon 2005). Relative air humidity also varies between sites with forest floor relative humidity ranging from 84 to 98 percent (Loescher *et al*. 2002) and canopy relative air humidity ranging from 69 to 100 percent (Cardelús & Chazdon 2005).

LITTERBAG EXPERIMENTS.—In the 'common substrate' experiment, I measured decomposition of cellulose Whatman #1 filters (Atlanta, Georgia), within the canopy and on the forest floor below the study branch to determine the effect of microclimate on decay rates. In the 'leaf litter' experiment, I decomposed native tree litter within its own canopy or on the forest floor below the study branch to determine *in situ* rates of litter decay.

The study tree species were *Dipteryx panamensis* (Pittier) Record & Mell (Fabaceae), *Hyeronima alchorneoides* Allemão (Euphorbiaceae) and *Lecythis ampla* Miers (Lecythidaceae). These species were chosen because they have varying leaf phenologies, are relatively abundant, are safe to climb and consistently have epiphyte cover. *Dipteryx* is dry season deciduous and has peeling bark, *Lecythis* is wet season deciduous and *Hyeronima* is evergreen. I selected four individuals of each species within a 1-h hike from the laboratory facility. The canopy soil nutrient status of study trees was examined in another study and found to vary significantly in N parameters among tree species and with season (C. L. Cardelús, C. Hinchliff & R. Sheedy, unpubl. data). Briefly, during the wet season, *Hyeronima*, the species with the highest litter lignin concentrations, had significantly greater net N-mineralization rates than *Lecythis* while no species had net N-mineralization in the dry season.

I collected litter from each sample tree in 2004 during the deciduous period of *Dipteryx* (February–March) and *Lecythis* (May) and over the course of a week for *Hyeronima* (February). I collected litter from *Hyeronima* by searching under the canopy for recently fallen leaves on multiple days. Freshly fallen *Hyeronima* leaves have a characteristic strong red or yellow color that quickly degrades (pers. obs.). For the deciduous species, I placed a tarpaulin under the canopy and collected newly fallen litter within 24 h. I chose litter that was free from insect and fungal damage. All litter was dried in the air-conditioned laboratory (*ca* 28°C) until the beginning of the experiment in January 2005.

Five grams of litter from each individual tree was set aside for initial litter chemistry analyses. The common substrate, 7 cm diameter filter paper, was weighed and sewn into 10 × 10 cm bags (1 mm mesh plastic window screening) and 5 g of individual tree leaf litter were weighed and sewn into 15 cm × 10 cm bags. One common substrate bag was then attached to one leaf litterbag and each set was labeled with a metal tag. A total of 60 common substrate and leaf litterbag pairs were deployed within the canopy and 60 litterbag pairs on the forest floor of four individuals of each study tree species. Litterbags deployed within the canopy were lain along one lower branch of each individual at a height of *ca* 20–25 m. Forest floor litterbags were placed on the ground beneath study branches, flagged and encircled with wire fencing to prevent trampling by animals. The standing litter pool on the forest floor and within the canopy was variable, thus in order to standardize placement, large, intact litter was removed before placing litter bags on the soil surface in each site.

One litterbag set was destructively harvested from each site on each of five sampling times: 32, 81, 152, 244 and 335 d after deployment. Litterbags were brought back to the field station and frozen (4°C) to stop microbial activity (Cornelissen *et al*. 2007). At the end of the experiment, the samples were air-dried in the laboratory (28°C), and shipped to the University of Florida for processing and analysis. All litterbags were gently rinsed with deionized water to remove any soil (Mack & D'Antonio 2003). Leaching of nutrients from rinsing would likely be minimal because these litterbags had all experienced at least 485 mm of rainfall in the first month of the experiment alone in which most of the leaching would occur. The filter or litter was then removed from the bag and picked through to remove invertebrates and roots, dried in the air-conditioned laboratory for 48 h and weighed. Samples were then dried in the oven at 60°C for 48 h and weighed again to determine oven-dried equivalent weight.

NUTRIENT ANALYSES.—Five grams of undecomposed litter from each individual tree and all dried litterbag litter were ground with a Wiley Mill (Thomas Scientific, Swedesboro, NJ) and passed through a #40 screen. Total percent carbon (%C) and nitrogen (%N) analyses were determined on a Costech Analytical Elemental Analyzer (Valencia, California). Total percent phosphorous (%P) concentrations were determined using an ash digestion (Jones &

Case 1996) followed by colorimetric analysis of ortho-phosphorous on an Astoria Pacific colorimetric autoanalyzer (Clackamas, Oregon). Initial litter lignin concentrations were determined using fiber analysis (ANKOM Technology, Macedon, NY, U.S.A.).

STATISTICAL ANALYSES.—I used one-way ANOVA and post hoc Tukey tests to compare initial litter chemistry among tree species. To compare the initial mass remaining over time [(mass t_x/initial mass) × 100] among species, for both the common substrate and litter experiments, as well as the percent C, percent N and percent P remaining over time for the litter experiment, I used a three-way ANOVA with species, site (canopy vs. forest floor) and time as main effects and a species × site interaction (Gartner & Cardon 2006). I also calculated the first-order litter decay constant, k, for each species (Swift *et al.* 1979). To compare the loss of N and P from the litter bags both within and between sites, I calculated the kN:kP ratio. If the result was > 1, then the rate of N loss was greater than that of P and if < 1, the rate of P loss was greater than N. I used linear regressions to determine if there were correlations between nutrient variables and litter decay.

RESULTS

Initial litter chemistry among tree species was variable (Fig. 1). *Dipteryx* had the highest percent N and percent P and the lowest C:N and N:P ratios. *Lecythis* had intermediate percent N, intermediate C:N ratios, the lowest percent P and percent lignin and highest lignin:P ratios. *Hyeronima* had the highest lignin:N and C:N ratios (Fig. 1).

COMMON SUBSTRATE EXPERIMENT.—The common substrate k was three times greater on the forest floor (5.7 ± 0.5), than within the canopy (1.9 ± 0.5) ($F_{24} = 4.64$, $P = < 0.001$) indicating faster decomposition rates in the former. There was no significant species × site interaction in the three-way ANOVA analysis, indicating that decomposition of the common substrate was not significantly influenced by tree species in either the canopy or forest floor sites ($F_{131} = 0.04$, $P = 0.96$). Within the canopy, 60 percent of the mass remained after 250 d, with the greatest mass loss occurring between 250 and 300 d when mass decreased by 30 percent, from 64 to 33 percent (Fig. 2). In contrast, on the forest floor, 28 percent of the initial mass remained after 32 d with zero mass remaining after 244 d (Fig. 2).

LEAF LITTER EXPERIMENT.—As predicted, overall litter decay rates were significantly slower within the canopy compared with the forest floor with an average k that was five times lower within the canopy, 0.76 ± 0.06, compared with the forest floor, 3.0 ± 0.46 ($F_{23} = 23.2$, $P = < 0.001$). *In situ* litter decomposed at different rates among tree species within sites as indicated by the significance of time and species and the significant species × site for mass loss (Table 1; Fig. 3). The rates of C, N and P loss were also significantly lower and less variable within the canopy than on the forest floor (Table 1; Fig. 3). Interestingly, the kN:kP ratios were significantly greater and more variable on the forest floor than within the canopy ($F_{21} = 13.5$, $P = < 0.001$). The kN:kP ratio varied between 0.6 and 1.2 on the forest floor and was consistently < 0.5 within the canopy indicating that P loss was consistently greater than N loss (Fig. 4).

Within the canopy after 12 mo, *Lecythis* litter had the most mass remaining (53 percent) followed by *Hyeronima* (47 percent), and *Dipteryx* with the least (41 percent) (Fig. 3). The litter decay constants, k, within the canopy were low (< 1) and significantly higher in *Dipteryx* than both *Hyeronima* and *Lecythis* (Table 2). The litter decay constant was also significantly and negatively correlated with initial litter lignin:P ratios (Fig. 5A) as well as positively correlated with initial P concentrations ($R^2 = 0.026$, $P = 0.067$). The pattern of C and N remaining was similar to that of mass, with the rank order *Lecythis* > *Hyeronima* > *Dipteryx* while rank order of initial P remaining was *Lecythis* > *Dipteryx* > *Hyeronima* (Fig. 3).

The forest floor litter mass and C, N and P loss, like the canopy, differed greatly among tree species (Fig. 3). For all variables measured over time, there was a significant effect of species and time, and a significant species × time interaction, with the exception of initial P remaining, for which there was no significant species effect nor species × site interaction (Table 1; Fig. 3). Although within the canopy, *Lecythis* had the highest initial mass remaining of the tree species, on the forest floor, *Lecythis* had the least initial mass remaining (2 percent), followed by *Dipteryx*, (15 percent), and *Hyeronima*, (20 percent; Fig. 3). *Lecythis*' greatest mass loss was during its leafless phase (Fig. 3). *Hyeronima* and *Dipteryx* had similar litter decay constants while *Lecythis'* was significantly greater (Table 2). Forest floor k's were significantly and negatively correlated with host tree litter initial percent lignin (Fig. 5B). The rank order of C and N remaining was consistent with initial mass remaining: *Hyeronima* > *Dipteryx* > *Lecythis*. The rank order changed with initial P remaining with *Lecythis* > *Dipteryx* > *Hyeronima*.

DISCUSSION

This is the first study to examine the effects of site (canopy and forest floor) and tree species on litter decay in a lowland tropical rain forest. The three main findings of this study are (1) decay rates within the canopy were significantly slower than on the forest floor for both substrata, which is likely due to differences in microclimate between sites; (2) the common substrate decay rates did not vary among tree species indicating that microclimate did not significantly effect decay rates within sites; and (3) *in situ* litter decay varied with tree species and site indicating different drivers of litter decay rates between the canopy and forest floor.

The significantly slower litter decay rates of both the common substrate and *in situ* litter in the canopy compared with the forest floor is likely due, in part, to its significantly lower humidity (J. E. Watkins, Jr., unpubl. data). This lower humidity is exacerbated by the rapid dry-down events of the canopy soil (Bohlman *et al.* 1995, Coxson & Nadkarni 1995), which negatively affects microbial activity (Maier *et al.* 1999) slowing down or halting the decomposition process for both the common substrate and leaf litter. The differences in water retention between the canopy and forest floor

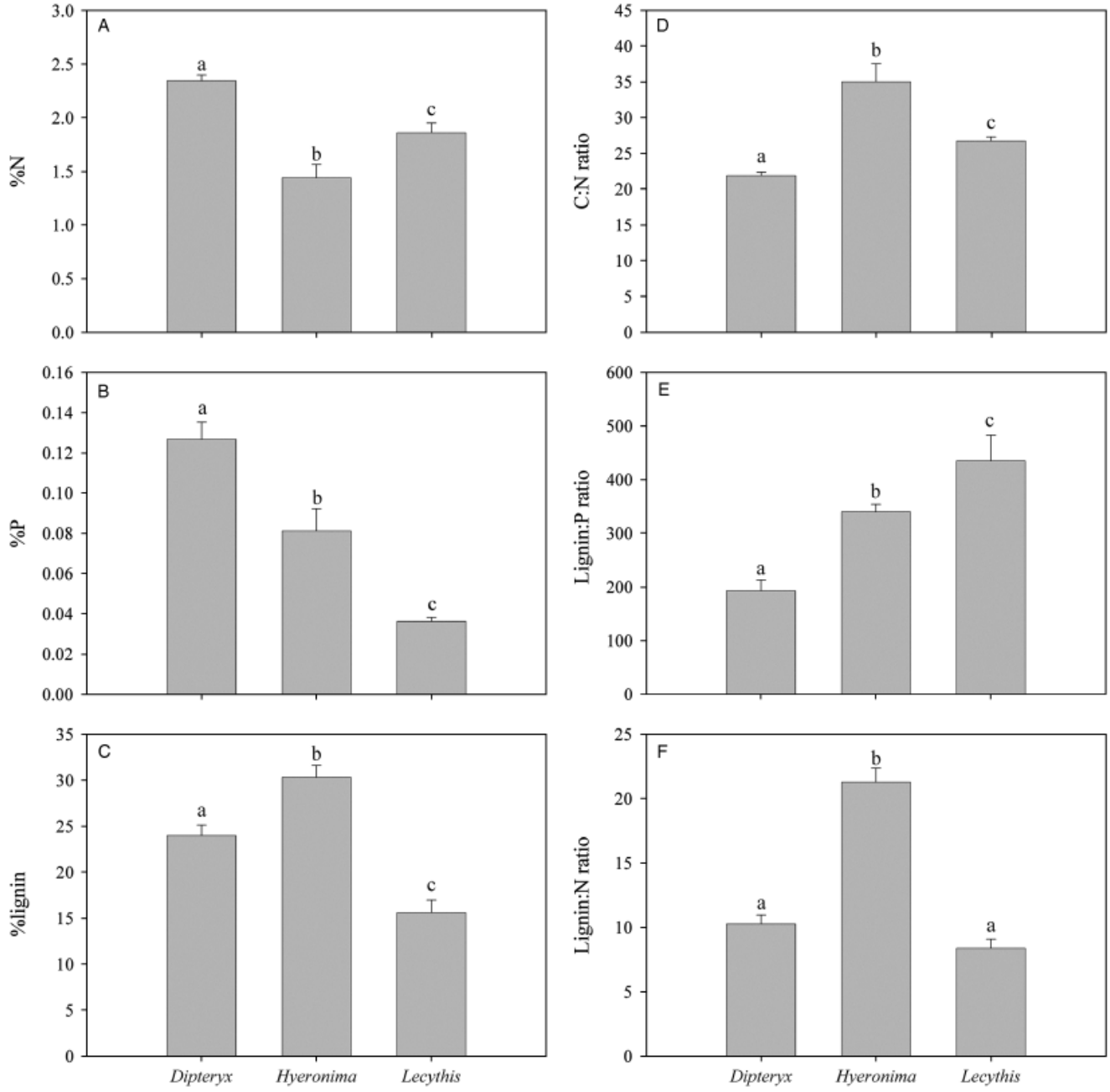

FIGURE 1. Mean (± SE) host tree litter percent nitrogen (A), percent phosphorous (B), percent lignin (C), C:N ratio (D), lignin:P ratios (E), and lignin:N ratios (F). Letters denote significant differences among species using a *post-hoc* Tukey test.

could also contribute to differential leaching of the litter and thus to the differences found in mass loss. Leaching is the first step of litter decay and is highest in sites with high precipitation (Swift *et al*. 1979, Currie & Aber 1997, Austin & Vitousek 2000). While precipitation rates were the same in the canopy and forest floor, forest floor clay soils are often water saturated which can lead to pooling on the surface and higher leaching from the forest floor litter layer (Sollins *et al*. 1994).

In line with mass loss differences between sites, losses of C, N and P from each tree species' litter were also significantly slower within the canopy than on the forest floor (Table 1; Fig. 3). Lignin:P ratio was the only nutrient variable that had a significant, negative and linear correlation with litter decay rates within the canopy while initial lignin had a significant, negative and linear correlation with litter decay on the forest floor. In the canopy, the greater the lignin:P ratio, the slower the rate of decay (Fig. 5A) and on the forest floor, the greater the lignin concentrations, the slower the rate of decay (Fig. 5B). Further evidence of the importance of P for canopy decay rates is reflected in the ratio of kN:kP. These ratios are < 0.5 within the canopy and indicate that P loss rates

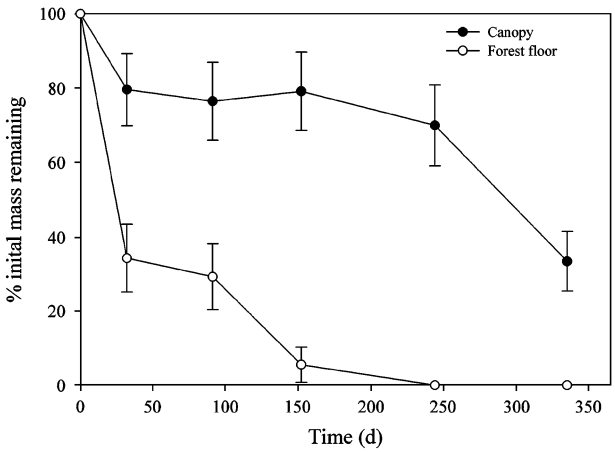

FIGURE 2. Mean (± SE) percent initial mass remaining of a common substrate decomposed in the canopy and forest floor of three tree species ($N = 12$) over 12 mo at La Selva Biological Station, Costa Rica. No significant differences were found among species within each site, so data were combined.

were greater than N loss rates whereas on the forest floor they are closer to 1 (Fig. 4). These results indicate that canopy microbes are immobilizing P from litter while forest floor microbes are likely immobilizing P from litter as well as from forest floor soil to facilitate decomposition. The tight link between canopy litter decay and P concentrations indicates P limitation to litter decay (Hobbie & Vitousek 2000).

The finding of P limitation to litter decay in the canopy is consistent with studies on canopy soil nutrients and epiphyte P limitation. Recent work comparing canopy and forest floor soil nutrient dynamics in the same tree species as this study show significantly greater total P and lower N:P ratios in forest floor soils compared with canopy soils (Cardelús *et al*. 2009). Studies on individual plant species demonstrate that P limits reproduction in one species of bromeliad (Zotz & Richter 2006) and is retranslocated more readily than N in multiple epiphyte species (Zotz 2004). There is also direct *in situ* evidence of P-limitation to epiphyte growth from montane forests in Hawaii where the abundance and diversity of nonvascular epiphytes increased significantly both when forest floor soils were fertilized with P and when canopy branches were fertilized directly with P (Benner & Vitousek 2007).

The greater P concentrations in forest floor soils compared with canopy soils are likely due to multiple factors including differences in pool size, storage capacity and access to 'new' P between sites. The soil pool size on the forest floor is greater than that within the canopy (5360, top 10 cm, vs. 1.85 t/ha, respectively, C. L. Cardelús unpubl. data) increasing the total pool size as well as storage capacity for P. Also, sources of new P from rock contribute > 50 percent of the P in forest floor soils (Porder *et al*. 2006); this forest floor P source is inaccessible to the canopy whose major sources of P is recyling via litter decomposition and throughfall.

Other important drivers that may contribute to the differences in litter decay rates between the canopy and forest floor include root density and meso- and macrofauna. Tropical trees can have a dense, shallow root layer that can grow into the litter layer where it is mechanically and chemically broken down (Sayer *et al*. 2006). The presence of such a layer could increase litter decay rates on the forest floor compared with the canopy. However, roots are also in direct contact with the litter layer in the canopy because epiphyte roots are literally what hold the canopy soil together and in place (pers. obs.). Thus, root density between sites may not vary nor have a differential affect on litter decay between sites. Litter fragmentation rates are more likely to vary between the canopy and forest floor because of the well-known differences in diversity and abundance of the micro- and mesofauna between sites (Nadkarni & Longino 1990, Nadkarni 1994, Erwin 1997, Ellwood & Foster 2004, Dial *et al*. 2006, Cardelús & Watkins in press). Whether forest floor micro- and mesofauna have a greater effect on litter decay than those in the canopy is unknown.

The between site comparison in litter decay clearly demonstrates that the canopy and forest floor have striking differences in litter decomposition due to differences in nutrient availability, microclimate and decomposer community. The differences in litter decay rates translate into differences in the rate at which nutrients are available to plants within each site. These differences are reflected in the variation in foliar nutrient chemistry between sites where canopy foliar tissue has significantly lower nutrient concentrations than those of the forest floor (Stewart *et al*. 1995, Hietz *et al*. 2002, Watkins *et al*. 2007).

Within sites, among species: Contrary to my hypothesis, the common substrate did not differentially decay among tree species within each site. I know from previous work that microclimate

TABLE 1. *Results of statistical comparisons using three-way ANOVA examining the effects of species, site (canopy and forest floor), time and a species × site interaction on initial mass loss and percent C, percent N and percent P initial mass loss of leaf litter in the canopy and forest floor habitats of three tree species at La Selva Biological Station, Costa Rica, over 12 mo.*

	% initial mass lost			% initial C lost			% initial N lost			% initial P lost		
Leaf Litter	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Model	10,130	17.6	< 0.001	10,130	17.5	< 0.001	10,130	7.28	< 0.001	10,114	10.2	< 0.001
Species	2	4.11	0.019	2	3.12	0.048	2	2.36	0.099	2	0.18	0.840
Site	1	21.1	< 0.001	1	28.1	< 0.001	1	18.6	< 0.001	1	12.3	< 0.001
Time	5	24.6	< 0.001	5	24.0	< 0.001	5	17.6	< 0.001	5	16.0	< 0.001
Species × site	2	5.05	0.008	2	3.66	0.029	2	2.82	0.064	2	0.45	0.638

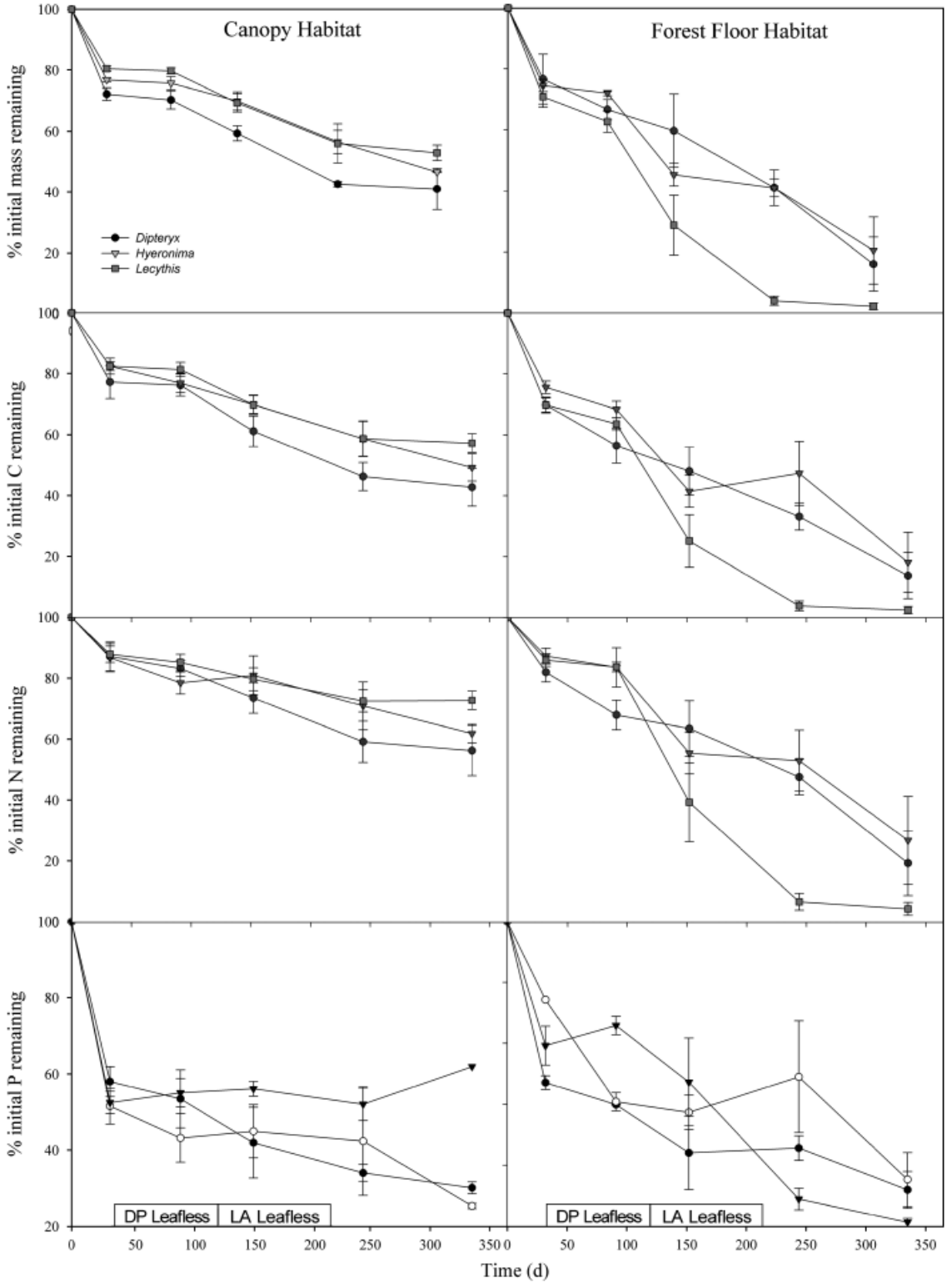

FIGURE 3. Mean (± SE) percent initial remaining mass (1st row), percent C (2nd row), percent N (3rd row) and percent P remaining (4th row) of each studied tree species' litter decomposed within its own canopy (1st column) or below their canopy on the forest floor (2nd column), at La Selva Biological Station, Costa Rica, after 12 mo. The period of leaflessness for *Lecythis* (LA) and *Dipteryx* (HA) is noted on the *x*-axis.

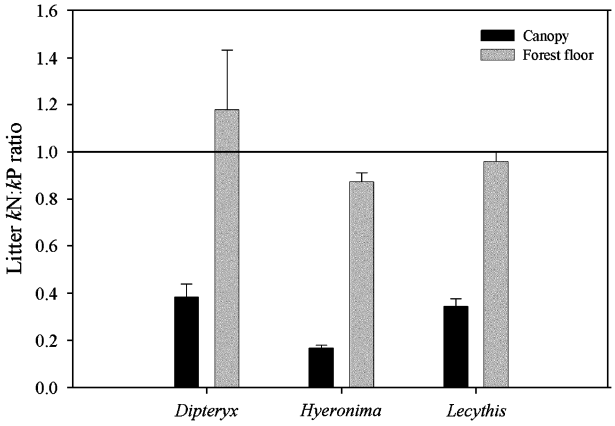

FIGURE 4. Mean (± SE) ratio of the litter decay constants, *k*, of N and P. Values < 1 (line) indicate greater rate of decay of P than N, while values > 1 indicate greater decay of N than P.

varies significantly between *Hyeronima* and *Lecythis* crowns throughout the year (Cardelús & Chazdon 2005), thus it is likely that *Dipteryx* would have a different microclimate as well, particularly because it is dry season deciduous. Although microclimate differs among tree species, it is possible that it is not different enough to affect decay rates of the common substrate differentially or that microclimate is not driving decay patterns in this ecosystem.

Unlike the common substrate experiment, in the litter experiment there was significant variation among species in mass and nutrient loss in both the canopy and on the forest floor. High C:N and lignin:N ratios are often indicators of low decomposition rates (Chapin 1980, Hobbie 1992, Parton *et al.* 2007), however, within the canopy there was little difference in *k*'s between *Hyeronima* and *Lecythis* given their dissimilarity in N litter chemistry (Table 2; Fig. 1). The species with the highest N and P concentrations, *Dipteryx*, had the highest decay rates, while the species with the lowest quality litter, *Hyeronima*, had comparable decay rates to *Lecythis*, the latter of which had the highest lignin:P ratio (Fig. 1). These data are consistent with the findings mentioned above that *P* variables, particularly lignin:P ratios, are a better indicator of decay rates within the canopy than N variables.

TABLE 2. *Linear regression results and decomposition constants* (k, *slope) of ln percent initial mass remaining on time for a each tree species leaf litter decomposed in the canopy and on forest floor for 1 yr at La Selva Biological Station, Costa Rica. Differences in lowercase letters indicate significant differences among species within a habitat* ($P < 0.05$) *and uppercase letters indicate significant differences within a species between sites (canopy and forest floor).*

Tree species	Site	df	*F*	*P*	R^2	*k* (yr^{-1})
Dipteryx panamensis	Canopy	1,17	97.0	< 0.001	0.85	0.91^{aA}
	Forest floor	1,23	22.1	< 0.001	0.48	2.45^{aB}
Hyeronima alchorneoides	Canopy	1,20	170	< 0.001	0.89	0.68^{bA}
	Forest floor	1,21	21.3	< 0.001	0.50	2.09^{aB}
Lecythis ampla	Canopy	1,16	133.4	< 0.001	0.89	0.66^{bA}
	Forest floor	1,23	123	< 0.001	0.84	4.38^{bB}

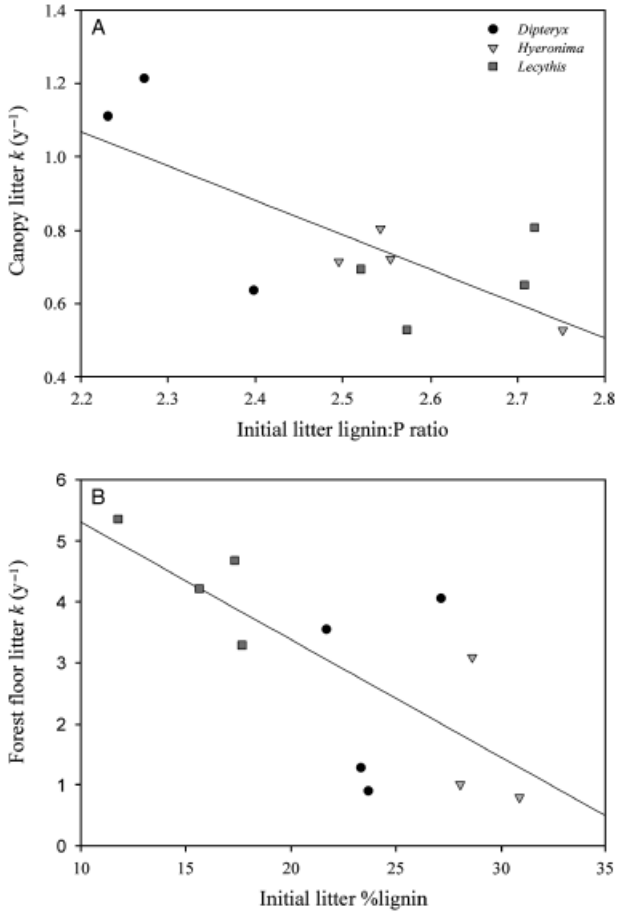

FIGURE 5. Linear regressions of (A) canopy litter decay constant, *k*, on initial litter lignin:P ratio and (B) forest floor litter decay constant, *k*, on initial litter percent lignin.

The rank order of litter mass loss over time was different on the forest floor where *Lecythis* had the greatest and *Dipteryx* and *Hyeronima* had similar rates (Fig. 3). *Lecythis'* low lignin and lignin:N ratio as well as intermediate N concentrations (Fig. 1) certainly favor it for higher decay rates than *Dipteryx* and *Hyeronima*. The rank order shift between *Lecythis* and *Dipteryx* between sites indicates, once again, that different litter chemistry variables are driving decay patterns between sites. In addition, *Lecythis'* most rapid mass loss occurred while it was leafless (Fig. 3). The sudden increase in light levels after leaffall could have promoted the photochemical breakdown of compounds without the adverse effect of drying out the soil because *Lecythis'* leaffall occurs during the wet season, however this effect was not seen with the common substrate.

This study demonstrates that the rate of nutrient inputs to canopy soil via litter decay is driven by litter quality and nutrient availability and not microclimate. While litter quality is well known to be an important determiner of decay rates (Swift *et al.* 1979), these differences among host tree species may have important

implications for the lowland canopy habitat. The foliar chemistry of epiphytes reflects low nutrient status and the potential inputs from host tree leaves could be an essential and important nutrient source. To this effect, the quality and quantity of litter inputs to the canopy habitat is important. The quantity of litter, as quality, likely varies with tree species. *Hyeronima*, which is evergreen, sheds leaves throughout the year likely contributing inputs consistently to the canopy habitat. *Dipteryx* sheds its leaves over the course of a month in the beginning of the dry season and remains deciduous for 2–3 mo; thus, inputs to the canopy would be high during leaf shedding period, and minimal throughout the rest of the year. *Lecythis* sheds all of its leaves over a 48 h period during the wet season and remains leafless for 2–3 mo. This final strategy would essentially provide one large input of leaves per year. This variation in inputs combined with differences in litter quality and microclimate likely results not only in known differences in canopy nutrient status among tree species (Cardelús *et al*. 2009) but also to variation in epiphyte species composition among tree species (Cardelús 2007) and ultimately to the high species richness of the epiphyte community.

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