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Leaf Litter Decomposition and Substrate Chemistry of Early Successional Species on Landslides in Puerto Rico[1]

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ABSTRACT

Decomposition is a critical process for nutrient release and accumulation of soil organic matter in disturbed soils, such as those found on landslides. I conducted a decomposition experiment on five landslides in the Luquillo Mountains of Puerto Rico as part of an investigation of the successional roles of two of the most common plant colonists to landslides, *Cecropia schreberiana* Miq. (Cecropiaceae) a pioneer tree species, and *Cyathea arborea* (L.) Sm. (Cyatheaceae) a pioneer tree fern. I compared leaf litter decomposition over one year and the initial and 1-yr chemistry for both species. Initial litter chemistry differed between the two species, as *Cecropia* had slightly higher nitrogen (9.2 mg/g) than *Cyathea* (8.2 mg/g) and higher lignin (28.6%) than *Cyathea* (26.0%), but water-soluble carbon and nonpolar extractable carbon (fats and oils, waxes, chlorophylls) were higher in *Cyathea* than *Cecropia.* Total carbon, acid-soluble carbon, total phosphorus, and pH did not differ significantly between leaf litter species. Across all five landslides, *Cyathea* ($k = 0.93 \pm 0.06$) leaves decomposed significantly faster than *Cecropia* ($k = 0.68 \pm 0.06$). The differences in these species leaf litter decomposition rates and chemical composition could potentially influence organic matter dynamics and nutrient cycling rates in these early successional systems.

RESUMEN

La descomposición es un proceso crítico para la liberación de nutrientes y la acumulación de materia orgánica en suelos perturbados, tales como los que se encuentran en derrumbes. Realicé un experimento de descomposición en cinco derrumbes en las Montañas de Luquillo en Puerto Rico para investigar el rol de sucesión dos plantas comunes en derrumbes, *Cecropia schreberiana* Miq. (Cecropiaceae) una especie de árbol pionero y *Cyathea arborea* (L.) Sm. (Cyatheaceae) un helecho arborescente pionero. Comparé la tasa de descomposición foliar durante un año, la química foliar incial y luego despues de un año para las dos especies mencionadas. La química foliar inicial difirió entre las dos especies, ya que *Cecropia* tenía el nitrógeno ligeramente más alto (9.2 mg/g) que *Cyathea* (8.2 mg/g) y la lignina más alta (28.6%) que *Cyathea* (26.0%), pero menos carbono soluble en agua y carbono no polar extraíble (grasas y aceites, ceras, clorofila). El carbono foliar total, carbono soluble en ácido, fósforo total y el pH no difirieron significativamente entre especies. A través de los cinco derrumbes, las hojas de *Cyathea* ($k = 0.93 \pm 0.06$) se descompusieron significativamente más rápido que las de *Cecropia* ($k = 0.68 \pm 0.06$). Las diferencias en las tasas de descomposición de estas especies y la composición química podrían potencialmente afectar la dinámica de la materia orgánica y el ciclo de los nutrientes en estos sistemas sucesionales tempranos.

Key words: Cecropia schreberiana; Cyathea arborea; decomposition; disturbance; foliar chemistry; landslides; lignin; litter quality; Puerto Rico; succession.

DECOMPOSITION IS A CRITICAL PROCESS FOR REGULATING NUTRIENT CYCLING and production in all ecosystems (Schlesinger 1997, Coleman *et al.* 2004). Landslides may be an extreme case of a system that depends heavily on decomposition of organic matter to provide carbon (C) and nutrients because of the general absence of these resources following disturbance (Guariguata 1990, Fetcher *et al.* 1996, Walker *et al.* 1996, Shiels *et al.* 2005). The dominant controls on decomposition in humid tropical forest are litter quality and the activity of soil biota (Lavelle *et al.* 1993, Aerts 1997, González & Seastedt 2001, Loranger *et al.* 2002). Litter quality, which is largely defined by litter chemistry, changes through succession. These changes in litter quality reflect changes in vegetation species composition (Facelli & Carson 1991, Facelli & Pickett 1991, Walker & del Moral 2003), and influence the rate of nutrient release and the dynamics of the biotic community (Hobbie 1992, 1996). Therefore, the quality of litter deposited into landslides may have substantial impacts on decomposition rates, and this will influence ecosystem development and primary succession.

Cecropia is one of the most well-studied tree genera in the Neotropics (Brokaw 1998), and is prevalent in disturbed areas, such as landslides, roadsides, and treefall gaps. *Cecropia* fits the paradigm of a "typical" early successional species, making it a species of interest for the studies of vegetation succession and disturbance ecology. Past studies in Puerto Rico have shown that *Cecropia schreberiana* Miq. (Moraceae) is the most abundant woody species on landslides (Myster & Walker 1997), and is one of the ten most common tree species in the Luquillo Mountains, having long-term effects on forest dynamics following large-scale disturbances such as hurricanes (Lawrence 1996, Brokaw 1998). Because of its ubiquitous occurrence in the Luquillo Mountains, as well as high growth rates (2.1 m in the first year of growth; Silander 1979) and litterfall rates (Zou *et al.* 1995), *Cecropia schreberiana* has generated interest by those studying decomposition and biogeochemical processes in the Luquillo Mountains (La Caro & Rudd 1985, González & Seastedt 2001, Fonte & Schowalter 2004).

Like *Cecropia*, the tree-fern *Cyathea arborea* (L.) J.E. Sm. (Cyatheaceae) is also one of the most common plant species present on landslides in the Luquillo Mountains (Guariguata 1990, Walker *et al.* 1996). Although much less studied when compared to *Cecropia schreberiana*, there are at least three species of *Cyathea* that are

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common to the forest understory of the Luquillo Mountains; *Cyathea arborea* is the dominant species of the genus that colonizes Puerto Rican landslides. Detailed studies of species in the genus *Cyathea* are absent or unpublished in Puerto Rico (but see Conant 1976), but a demographic study of *Cyathea arborea* on landslides shows that leaf production and turnover rates are among the highest for tree ferns in the tropics (L. Walker, pers. comm.).

Cecropia schreberiana and *Cyathea arborea* are dominant species on Puerto Rican landslides (Walker *et al.* 1996), top contributors to litterfall in <13-yr-old landslides (A. Shiels, pers. obs.), and both experience fast growth rates (Silander 1979, Brokaw 1998, L. Walker, pers. comm.). Despite the overlapping characteristics of these two pioneer species, understanding the leaf litter chemistry and decomposition rates will help determine individual roles in nutrient cycling and primary succession on landslides. The objectives of this study were to compare the litter quality (leaf litter chemistry) of *Cecropia schreberiana* and *Cyathea arborea*, and to compare the decomposition rates of these two species over a 1 yr period across several very different, yet representative, landslides in the Luquillo Mountains in Puerto Rico.

METHODS

STUDY SITE.—This study was conducted on five landslides in the Luquillo Mountains in northeastern Puerto Rico (18°18′N, 65°50′W). The Luquillo Mountains are approximately 11,000 ha of montane forest, with mean annual precipitation of 3000–4000 mm, and mean monthly temperatures ranging 21–25°C (Brown *et al.* 1983, Soil Survey Staff 1995). The landslides used in this study were between 460 m and 750 m a.s.l and extend across two major forest types resulting from the altitudinal gradient present in the Luquillo Mountains. Below 600 m elevation the vegetation is subtropical wet forest (Ewel & Whitmore 1973), and above 600 m the vegetation is subtropical rain forest (Waide & Lugo 1992). Landslide vegetation is dominated by high-light tolerant species typical of early succession, including several types of grasses (*e.g., Andropogon, Paspalum*), tree ferns (*Cyathea*), and climbing ferns (*Dicranopteris, Gleichenia*), as well as woody colonizers, such as *Cecropia, Miconia*, and *Tabebuia* (Myster & Walker 1997, Shiels & Walker 2003). Vegetation nomenclature follows Taylor (1994).

Five landslides were chosen at random among all landslides in the Luquillo Mountains that had <30° slopes (14–27°), had an area of bare soil (<20% plant cover) at least 14 m^2, and that were accessible (<500 m from a road or trail). The landslides were underlain by two different soil types, as two landslides (RB10 and MY8) were Inceptisols derived from quartz-diorite bedrock, and the other three landslides (ES5, ES10, J4) were Ultisols derived from volcaniclastic bedrock (Seiders 1971). Landslides were defined by watersheds (Río Espíritu Santo = ES, Jiménez = J, Río Blanco = RB, and Río Mameyes = MY, and numbers used in other landslide studies, *e.g.*, see Myster & Walker 1997, Shiels & Walker 2003).

To characterize the landslide soil environment, soil samples were taken on 10 August 2001 from 10 cm depth at three random locations that were at least 50 cm away from any litterbag in each landslide. Soil was then analyzed for moisture (proportion of dry mass), organic matter (proportion lost on ignition), bulk density, particle size (Sheldrick & Wang 1993), pH (1:1 paste of soil and de-ionized water), and total nitrogen (N) and phosphorus (P) (Kjeldahl digestion followed by colorimetric analysis; Alpkem Corporation 1992). Incoming light for each landslide was determined by averaging three measurements at ground level on a cloudless day with Li-Cor quantum photometer model LI-185B (LI-COR, Inc., Lincoln, NE, USA).

TREATMENTS.—Recently senesced leaves of *Cecropia schreberiana* and *Cyathea arborea* were collected from roadsides in the Luquillo Mountains, dried at 40°C to a constant weight, and cut into pieces approximately 2 cm^2 to create a homogenous sampling pool for each species. Decomposition bags (litterbags) were constructed using fiberglass screening (1.2 mm mesh). Although litterbags are commonly used to compare decomposition rates between species, the use of litterbags excludes soil macrofauna and therefore may underestimate true rates of litter decay. A total of 5 g of single-species leaf material was added to each 12 cm × 10 cm litterbag in proportions representative of their natural leaf parts (*Cecropia*: 21.5% petiole, 78.5% blade; *Cyathea*: 66.5% rachis, 33.5% pinnae; see Shiels 2002). Instead of attempting to separate leaf parts for each collection period, total remaining biomass was determined after each litterbag collection.

A total of 150 litterbags (5 landslides × 5 sampling periods × 3 replicates × 2 species) were constructed, filled, and placed on the soil surface, allowing >20 cm distance to rocks or edges of established vegetation but in areas that could be easily accessed, on the upper, vegetation-free portions of the five landslides. Each litterbag was held in position by driving a galvanized metal 14 cm nail into the ground and attaching a metal wire to the litterbag and nail. Buffer zones of at least 10 cm in each direction separated adjacent litterbags. To account for handling loss, the first set of litterbags was collected immediately upon placement at each site on 10 August 2000. The remaining litterbags were collected after 65, 150, 300, and 365 d. Upon collection, each litterbag was washed to remove soil, keeping the foliar material inside the bags and then dried at 40°C for 3 d. This washing and drying procedure was repeated two more times in order to remove all visible soil that had accumulated on the foliar material during the study. Each sample's foliar material was weighed and recorded upon final cleaning and drying, and percent remaining biomass was calculated as a portion of the initial dry littermass. Additionally, decomposition rate constants (*k*-values) were calculated for each leaf species on each landslide using the negative exponential model: $Y = e^{-kt}$, where Y is the proportion of initial littermass remaining at time period t (in years), and k is the decomposition factor, or slope fitted to the data (Swift *et al.* 1979).

LITTER CHEMISTRY.—Chemical analyses of *Cecropia* and *Cyathea* were conducted on samples ($N = 3$ for each species) of initial litter (0 d of decomposition). Sequential C analysis was conducted at the Center for Water and the Environment (University of Minnesota, Duluth, Minnesota) using a standardized forest products procedure

(Ryan *et al.* 1989) to determine the following fractions: nonpolar extractives (fats, oils, waxes, and chlorophylls), water solubles (amino acids, simple sugars, and soluble phenolics), acid solubles (cellulose, hemicellulose, starch, polypeptides, and nucleic acids), and acid insolubles (lignin). All C fractions are reported on an ash-free dry mass basis. Total N and total P were determined using the same methods as soils (see above) for both initial litter samples and on decomposed litter from the 365 d sampling.

STATISTICAL ANALYSIS.—Remaining biomass of *Cecropia* and *Cyathea* were analyzed for 60, 150, 300, 365 d sampling periods using a mixed-model repeated-measures MANOVA where the two litter species were fixed effects and the five landslide sites were random effects. Leaf litter N and P at 365 d after litterbag additions were compared between *Cecropia* and *Cyathea* with mixed-model two-way ANOVAs. Decomposition rate constants (*k*-values), initial *Cecropia* and *Cyathea* litter chemistry, and pH were compared using *t*-tests.

For all analyses, significant ($P < 0.05$) multivariate comparisons, determined by Wilks' Lamda values (all multivariate test statistics were concordant), were followed by two-way ANOVAs, or one-way ANOVAs for each sampling period. Type III sum of squares was used for all parametric tests in order to adjust for all effects including interactions (SAS Institute 1996). Tukey's post-hoc test was also performed when a significant ($P < 0.05$) F value was found. All analyses used General Linear Models procedures of SAS (SAS Institute 1996), except for initial litter chemistry that used JMP (JMP 2000), and variables were checked for normal distribution and equal variance before parametric tests were conducted. Significant site (*i.e.*, landslide) effects were reported but not discussed because the main focus of the experiments was to test for species differences over the five different sites. Therefore, significant species and significant site × species interactions were the focus of this study.

RESULTS

Decomposition rate over one year differed significantly between the two species, with *k*-values of 0.68 ± 0.06 for *Cecropia* and 0.93 ± 0.06 for *Cyathea* ($t = 3.08$; df = 1; $P = 0.01$; Fig. 1). For both species combined, the mass remaining differed among landslides ($P = 0.004$; interaction term not significant), which may have been influenced by the widely varying environmental conditions that were measured on the five landslides (Table 1). Additionally, the sampling period (time) affected decomposition rates as there was a site × species interaction for 60 d ($P < 0.001$) and 150 d ($P = 0.04$) after the onset of the experiment. After 60 d, the significant interaction appeared to be a result of lower *Cyathea* values on the ES5 landslide than values in all other landslides, whereas after 150 d, the significant interaction appeared to result from low values for *Cecropia* on the RB10 landslide (data not shown).

Leaf litter chemistry was different between the two species as nonpolar extractable C ($t = 4.36$; df = 4; $P = 0.01$; Table 2) and water soluble C ($t = 7.16$; df = 4; $P = 0.002$) were significantly

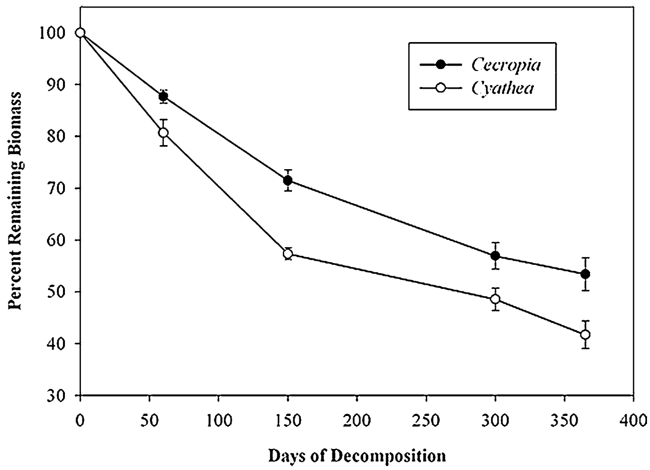

FIGURE 1. Mean (± SE) percent mass remaining of *Cecropia* and *Cyathea* leaf litter for each collection period (60, 150, 300, 365 d) on five landslides in the Luquillo Mountains, Puerto Rico. Species were significantly different when averaged through the 1 yr study ($P < 0.001$).

higher in *Cyathea* than *Cecropia*. Lignin (acid insoluble C) was significantly higher in *Cecropia* leaves than in *Cyathea* leaves ($t = 3.58$; df = 4; $P = 0.02$), whereas acid soluble C did not differ between species ($P > 0.05$). Initial (undecomposed) *Cecropia* litter had approximately 0.10 percent greater N than initial *Cyathea* litter ($t = 3.29$; df = 4; $P = 0.03$), but total C, total P, and pH did not differ significantly between species ($P > 0.05$; Table 2).

Interestingly, the N remaining in litterbags (as a percentage of initial N) after 1 yr was three times higher in *Cecropia* litter (65.1 ± 8.0%) than in *Cyathea* litter (19.6 ± 2.3%). The species were similar for P (*Cecropia* 29.4 ± 7.5%; *Cyathea* 24.0 ± 6.9%). When nutrient concentrations were not adjusted for mass loss over 1 yr, *Cecropia* litter had a similar N concentration as undecomposed *Cecropia* (10.12 ± 0.95 mg/g), but *Cyathea* N (3.87 ± 0.32 mg/g) decreased by approximately 50 percent. Furthermore, when N and P were compared between *Cecropia* and *Cyathea* after 1 yr of decomposition, *Cecropia* had significantly higher N than *Cyathea* ($P < 0.001$). This was not the case with remaining P, however, as total P was similar initially and after 1 yr when *Cecropia* (0.12 ± 0.02 mg/g) and *Cyathea* (0.12 ± 0.03 mg/g) were compared ($P > 0.05$). Finally, there was a significant site × species interaction for total N ($P = 0.05$), supported by a lack of treatment difference on landslide J4 (data not shown).

DISCUSSION

Cyathea leaves decomposed 10 percent faster than *Cecropia* leaves when averaged across all landslides and sampling dates despite very different site condition (Table 1). Litter quality differences between the two species provide the strongest explanation for the differences in decomposition rates, supporting past conclusions in wet tropical environments (Lavelle *et al.* 1993, Aerts 1997, Loranger *et al.* 2002).

TABLE 1. *Environmental characteristics for the five landslides in the Luquillo Mountains, northeastern Puerto Rico. Soil was sampled to 10 cm depth at each site (mean ± SE;* N = *3).*

	Landslide				
	ES5	ES10	J4	RB10	MY8
Parent material	Volcaniclastic	Volcaniclastic	Volcaniclastic	Quartz-diorite	Quartz-diorite
Elevation (m a.s.l.)	580	600	460	600	750
Area (m^2)	2923	1440	1457	810	1512
Light (μ Einsteins/m^2/s)	2267	1750	2050	1867	2167
Soil properties					
Total N (μg N/g soil)	96.69 ± 40.07	564.04 ± 235.61	163.96 ± 25.11	759.95 ± 149.57	97.21 ± 26.12
Total P (μg P/g soil)	380.63 ± 89.37	308.30 ± 90.71	180.17 ± 26.29	77.44 ± 3.89	242.81 ± 39.47
Organic matter (g/g)	0.13 ± 0.00	0.16 ± 0.01	0.15 ± 0.01	0.06 ± 0.01	0.08 ± 0.01
Sand (g/g)	0.61 ± 0.00	0.50 ± 0.02	0.59 ± 0.03	0.80 ± 0.01	0.81 ± 0.02
Silt (g/g)	0.17 ± 0.01	0.14 ± 0.03	0.16 ± 0.02	0.07 ± 0.01	0.15 ± 0.01
Clay (g/g)	0.22 ± 0.01	0.36 ± 0.03	0.25 ± 0.02	0.13 ± 0.00	0.04 ± 0.01
pH	4.78 ± 0.21	4.22 ± 0.13	4.48 ± 0.02	4.68 ± 0.12	4.67 ± 0.06
Moisture (g/g)	0.58 ± 0.02	0.43 ± 0.01	0.51 ± 0.02	0.42 ± 0.04	0.38 ± 0.02
Bulk density (g/cm^3)	0.95 ± 0.03	0.94 ± 0.02	0.97 ± 0.01	1.29 ± 0.10	1.00 ± 0.07

Environmental conditions of the landslides minimally influenced decomposition patterns between the two species, as shown by the consistency of *Cyathea* decomposing faster than *Cecropia* at all sites and thus the lack of a site × species interaction. Given these findings, both *Cecropia* and *Cyathea* are expected to contribute to landslide succession differentially through their loss and retention of the critical resources (C and nutrients) from senesced leaves, and their contributions are expected to be consistent across highly variable landslides in the Luquillo Mountains.

The C chemistry of *Cyathea* foliar material had higher proportions of water soluble compounds when compared to *Cecropia* litter. The water soluble fraction is the most labile C, and therefore it is often the first to degrade (Paul & Clark 1989). When Allison and Vitousek (2004) examined leaf litter nutrients, enzyme activity, and C chemistry (using the same C fractionation method as in my study) for 11 plant species in Hawaii, they determined that water soluble C was the best predictor of decomposition rates. Fats, oils, waxes, and chlorophylls (nonpolar extractables) are also among the first foliar compounds to degrade (Paul & Clark 1989), and these C compounds were in higher concentrations in *Cyathea* litter than *Cecropia* litter. Nitrogen and lignin content of leaf litter have long been recognized as two of the most important chemical determinants of decomposition rates (Melillo *et al.* 1982, Coûteaux *et al.* 1991, Coleman *et al.* 2004), but litter N was not a good predictor of plant litter decomposition in this study, shown by higher initial and ending (after 1 yr decomposition) N concentrations of *Cecropia* compared to *Cyathea*. Lignin concentrations of both landslide species are relatively high when compared to other plant species in the Luquillo Mountains (La Caro & Rudd 1985, D.J. Lodge, pers. comm.), and several studies show that lignin content has more control than N over decomposition rates (Singh 1969, Fogel & Cromack 1977, La Caro & Rudd 1985, Bloomfield *et al.* 1993). However, lignin requires the presence of specific decomposers (especially basidiomycete fungi; Higuchi 1985, Swift *et al.* 1979) and because of this, lignin is generally the last in the sequence of C chemistry to degrade. Soil fungal communities are often at low levels on recent landslides, and probably absent initially after the landslide occurs (Calderon-González 1993, D.J. Lodge, pers. comm.). Therefore, the difference in lignin concentration between *Cecropia* and *Cyathea* may not have been as important as water soluble and nonpolar extractable compounds in contributing to the differences in decomposition rates between the species in this study.

Leaf litter decomposition rate constants (*k*-values) were low for both *Cecropia* and *Cyathea* when compared to past studies in the Luquillo Mountains (Zou *et al.* 1995, González & Seastedt 2001,

TABLE 2. *Leaf litter chemistry (mean ± SE) for* Cecropia schreberiana *and* Cyathea arborea. *Foliar material represents senesced leaves before decomposition on five landslides in the Luquillo Mountains, Puerto Rico. An asterisk (*) indicates a significant ($P < 0.05$) difference between leaf types (*N = *3). Acid insoluble C is equivalent to lignin.*

Leaf litter chemistry	*Cecropia*	*Cyathea*
N (mg/g)	9.24 ± 0.09	8.18 ± 0.31*
P (mg/g)	0.21 ± 0.03	0.21 ± 0.01
pH	5.27 ± 0.01	5.17 ± 0.00
C (%)	49.51 ± 0.16	50.38 ± 0.35
Water soluble C (%)	12.82 ± 0.35	17.12 ± 0.49*
Nonpolar extractable C (%)	4.69 ± 0.16	6.12 ± 0.29*
Acid soluble C (%)	53.86 ± 0.78	50.75 ± 0.92
Acid insoluble C (%)	28.64 ± 0.40	26.01 ± 0.61*

Myster & Schaefer 2003). However, this is not surprising given the few decomposer organisms and severe environmental conditions present following a landslide (Calderon-González 1993, Walker *et al.* 1996). *Cyathea* decomposition studies are unavailable and foliar information is limited; however, Allison and Vitousek (2004) found that leaves of the Hawaiian tree-fern *Cibotium glaucum* decomposed more slowly and contained much higher acid insolubles (lignin) and less water soluble C compounds than all six species of angiosperms in their study. This suggests that tree ferns, as a life form, not only differ in their foliar chemistry and decomposition, but may also have different impacts on nutrient cycling and ecosystem function in their respective ecosystems (Richardson *et al.* 2005; L. Walker, pers. comm.). Remaining *Cecropia* biomass in my study (88% after 65 d; 53% after 1 yr) was similar to past *Cecropia* decomposition studies in the forest understory in the Luquillo Mountains (80% after 65 d; La Caro & Rudd 1985; *ca* 40% without, and *ca* 65% with macroinvertebrates excluded after 1 yr; González & Seastedt 2001). In a decomposition experiment on a landslide in the Luquillo Mountains, which used three common leaf species of different stages of succession (*Cecropia schreberiana* = early; *Miconia racemosa* = mid; *Dacroydes excelsa* = late), all species lost approximately 45 percent of their original mass within 112 d (Myster & Schaefer 2003). In my study, only *Cyathea* lost comparable organic matter in that time frame, as *Cecropia* lost less than 30 percent organic matter during the same time period. This difference between rates of decomposition between studies using *Cecropia* could be attributed to Myster and Schaefer (2003) using a single landslide that was *ca* 10-yr old, whereas the five landslides in my study were on bare soil that had eroded less than 2 yr prior to my study.

Environmental conditions, such as different soil types, temperature, and moisture regimes change across the elevation gradient present in the Luquillo Mountains and in turn alter ecosystem processes such as decomposition and plant production (Waide *et al.* 1998). However, in this study, species differences for decomposition are consistent across widely ranging landslide conditions. This supports the conclusions of Myster and Schaefer (2003) that the species of leaf litter has a greater impact on decomposition rates than the location and environmental conditions on the landslide in the Luquillo Mountains.

The differing decomposition rates and nutrient dynamics of *Cecropia* and *Cyathea* will likely influence the patterns of biotic colonization and plant succession in these highly disturbed sites in the Luquillo Mountains. With accelerated decomposition, it might be expected that *Cyathea* leaves would have greater positive influence on landslide succession because of the faster release of resources than *Cecropia* leaves. However, fast release of C and nutrients in a wet environment that lacks biota may result in loss, perhaps through leaching, of these important resources, and this may have been the case in a previous landslide study in Puerto Rico where litter additions did not increase available soil nutrients (Shiels *et al.* 2005). In landslides with minimal biota to take up nutrients, *Cecropia* might have more positive effects on succession because of the slower decay of organic matter that contains higher initial and 1-yr N concentrations.

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