



Species and microsite effects on litter decomposition in a Puerto Rican landslide

R. W. Myster^{1,3} and D. A. Schaefer²

¹*Department of Biology, Box 89, University of Central Oklahoma, Edmond, OK 73034 USA*

E-mail: rmyster@ucok.edu

²*412 Ventura Way, Claremont, CA 91711 USA*

³*Corresponding author.*

Keywords: Lower montane wet forest, LTER, Luquillo Experimental Forest, Nutrient immobilization.

Abstract: Because decomposition is an important ecosystem process and species control of it is an issue in the tropics, we examined how much plant species controlled decomposition compared to environmental conditions on a landslide in Puerto Rico. We chose a landslide because of its extreme spatial variation in environmental conditions, and found that the landslide center microsite had the greatest variation in temperature and precipitation. Litterbags were filled with single-species leaves of three different plant species and placed in center, border and forest landslide microsites. Bags were collected after 1, 2, 4, 8 and 16 weeks and analyzed for organic matter and various other chemicals. All chemicals showed strong differences among plant species and very little significant environmental variation and, with one exception, organic matter loss followed the same exponential decay pattern for all species and microsites. Interestingly, nitrogen (N) and phosphorus (P) immobilization was seen for all three litter types, and calcium immobilization was seen for two of the three. However, immobilization of N and P were most pronounced for the early successional species. Finally, the dominance of species effects over environmental effects suggests that leaf litter chemistry strongly influences decomposition in landslides. While the soil decomposer biota act similarly along landslide environmental ranges, they are more responsive to substrate quality.

Introduction

Decomposition is an important process in tropical forests (La Caro and Rudd 1985, Zou et al. 1995). Those forests are often on nutrient-poor soils with relatively low external nutrient inputs, where most of the nutrients released by decomposition are rapidly reclaimed by plants and the soil biota, retaining them within the system (Vitousek et al. 1982, Vitousek 1984). Tropical forests are appropriate for examination of control of decomposition because: (1) of their rapid nutrient turnover rate (Olson 1963, Vitousek 1984), (2) tropical ecosystem functions may depend strongly on individual species and their interactions (Brown and Lugo 1982) also true in the temperate zone (Wardle et al. 1997), and (3) areas of severe disturbance are common in the tropics, allowing examination of abiotic mechanisms due to the resulting substantial spatial variation of temperature, light, soil moisture and nutrient availability within them (e.g., landslides often contain exposed nutrient-bearing weatherable saprolite; Myster and Fernández 1995).

Consequently to address the objective of better understanding controls (both abiotic and biotic) on tropical decomposition, we set out weather stations and litterbags on a landslide in Puerto Rico and answered these questions:

- (1) What are the air and soil temperature, humidity and rainfall on landslide and adjacent forest microsites over a 16-week period in Puerto Rico?
- (2) What is the rate of organic matter loss in litterbags containing leaves of three tropical trees of differing successional status placed in these microsites over the same 16-week period?
- (3) Are these patterns, among species and among microsites, different for loss rates of potassium, nitrogen, phosphorus, calcium and magnesium?

Materials and methods

The study site was the Luquillo Experimental Forest (LEF) of northeastern Puerto Rico USA (18° 20'N, 65° 45'W). The LEF is the tropical long-term ecological re-

search site of the National Science Foundation (LTER), consisting of tropical lower montane wet forest (Holdridge 1967). We chose for study a landslide located in Tabonuco forest at 370 m elevation in the Río Espíritu Santo watershed, which slid most recently in 1986 (E2: also used in Myster and Fernandez 1995). This landslide has an area of 1555 m², an average width of 75 m, a 49° aspect and a 30° slope (Guariguata and Larsen 1990). Like all landslides, it has rock and bare soil (with loss of soil profile) patches in the top portion of the slide, and both tree and soil debris in the lower portion of the slide (Myster 2002b). Twelve landslide and adjacent forest microsites, previously sampled for light and soil nutrients (Fernandez and Myster 1995, Myster and Fernandez 1995), were selected: landslide center (C), landslide border 2 m from the forest border (LB), forest border with the landslide (FB) and forest (F), on each of three transects 10 m, 20 m and 30 m from the top of the slide (see Myster and Fernández 1995, for light and soil information on these microsites). Three self-contained weather stations were placed in three of the 12 microsites: in the center of the landslide 10 m from the top, at the landslide/forest border just inside the landslide 20 m from the top and in the forest 30 m from the top, and measurements were taken 1.5 m above the soil surface.

We constructed 180 (12 microsites × 5 sample periods × 3 species) 20 cm × 20 cm litterbags of 1 mm steel mesh on top to permit soil faunal access, and 0.01 mm mesh synthetic cloth on the bottom to prevent small litter fragments from falling out (as in other Puerto Rican decomposition studies: Zou et al. 1995, Lui and Zou 2002, Myster 2002a). In addition, we used ash measurements and expressed results as ash-free weight to exclude the effect of transport of inorganic soil particles into the bags. One species from each broad successional stage was chosen for the experiment. We filled 60 bags with recently fallen unwashed leaves of *Cecropia schreberiana* (a common early successional LEF species: Myster 2002a,b), 60 bags with *Miconia racemosa* (a common mid-successional LEF species: Myster 2002a) and 60 bags with *Dacryodes excelsa* (a common late successional LEF species and the dominant species of the tabonuco forest: Myster and Walker 1997).

The leaves were oven-dried at 65° C for 48 h and then 10 g of the dried plant material was put into each bag without breakage. Five bags of each species were placed in each microsite on March 1, 1996, atop the decomposing litter layer with a few freshly-fallen leaves put on top, and one bag of each species in each microsite was collected 1, 2, 4, 8 and 16 weeks later. The initial litter of each species and contents of the collected litterbags were dried, milled

to 1.0 mm mesh, and subsamples ($n = 3$) consumed in a furnace (550°C for 12 hr) to determine ash-free dry weight and percent of the organic matter remaining. Chemical analyses of subsamples were done for total nitrogen (N) by combustion analysis, and phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) by inductively coupled plasma spectroscopy after H₂O₂ and HNO₃ digestion (Luh-Huang and Schultz 1985). These data were converted to percentage of the initial organic matter and nutrient remaining within each litterbag.

For all chemical response parameters, Repeated Measures Analysis of Variance (ANOVA for main effects only) was performed because measurements were not statistically independent, and the Ryan-Einot-Gabriel-Welsch multiple-range test was used to investigate differences between levels of the main effects (SAS 1985). To investigate the species main effects, we pooled samples mathematically over the microsites producing 12 replicates at each of the five sampling periods. Likewise for the microsite main effects, we pooled samples over the species producing three replicates at each of the five sampling periods. That is, replication was achieved for species by pooling across microsites, and for microsites by pooling across species. However, species × microsite interaction effects were not examined because of insufficient replication. Due to the large number of tests, a sequential Bonferroni test was employed (Rice 1989) to suggest if any significant results should be viewed with suspicion. The significance of differences in the decay constant for organic matter (k value: Weider and Lang 1982) was tested using one-way ANOVA (SAS 1985). The k constant was calculated by taking the logarithm of the entire % initial mass remaining values and regressing them against time in the field (in years). The slope of that regression is k , usually expressed as a positive value, and its units are years⁻¹.

Results

Among the three sampled microsites, the landslide center microsite had the lowest daily minimum air temperature (18.2°C vs. 18.6°C border and 19.0°C forest), the highest daily maximum air temperature (29.3°C vs. 26.0°C border and 25.3°C forest), the highest soil/litter interface temperature (21.5°C vs. 20.8°C in both border and forest), and the highest precipitation (1390 mm vs 970 mm border and 830 mm forest). The 16-week study period had above-average precipitation. Only relative humidity of the air, measured at 1.5 m above the soil surface, was greater in the forest microsite (72% minimum/100% maximum vs. 63%/94% border and 49%/94% landslide). Initial leaf litter analyses showed that N was highest in

Table 1. F statistic summary with level of significance indicated by a “*” for $0.05 < p < 0.01$, a “***” for $0.01 < p < 0.001$ and a “****” for $0.001 < p < 0.0001$. No superscript denotes that no significant difference was found. The degrees of freedom for species ANOVAs was 2 and for microsite ANOVAs was 11.

Time	Source of variation	Org	K	N	P	Ca	Mg
1 week	species	1	22***	38***	29***	57***	32***
1 week	microsite	1	1	2*	1	1	1
2 weeks	species	2	30***	20***	16***	56***	21***
2 weeks	microsite	2	1	2*	1	1	1
4 weeks	species	5*	27***	4*	28***	90***	29***
4 weeks	microsite	1	2	1	1	1	1
8 weeks	species	1	28***	16***	16***	36***	16***
8 weeks	microsite	1	1	1	1	1	1
16 weeks	species	1	9**	15***	10**	37***	15***
16 weeks	microsite	1	1	1	2	1	1

Cecropia (11.5 g kg^{-1} vs. 8.1 g kg^{-1} in *Dacryodes* and 7.9 g kg^{-1} in *Miconia*), that Ca and Mg were highest in *Miconia* (22.6 and 3.8 g kg^{-1} vs. 13.0 and 2.8 g kg^{-1} in *Cecropia*, and 7.3 and 1.1 g kg^{-1} in *Dacryodes*), and that P and K decreased in the order *Cecropia* (0.43 and 6.8 g kg^{-1}) > *Miconia* (0.24 and 4.4 g kg^{-1}) > *Dacryodes* (0.12 and 1.2 g kg^{-1}).

Percent organic matter remaining was significantly different among species only after 4 weeks in the field (Table 1), but it was not different when using all data (same as Wardle et al. 1997). Multiple-range testing of species levels at this 4 week period showed that all species were significantly different (this was also the case for every significant species effect in Table 1); *Dacryodes* lost organic matter fastest (70%) remaining with *Cecropia* second (80%) and *Miconia* third (88%; Fig. 1a). The exponential decay coefficient for organic matter loss was significantly different among species ($df = 2$, $F = 2.99$, $p = 0.05$) but not among microsites ($df = 11$, $F = 1.05$, $p = 0.44$). In addition, means testing showed that *Dacryodes* was most different from the other species. For all three species averaged together, k was 2.2 ± 0.2 , similar to the 1.9 ± 0.2 calculated from the data in Zou et al. (1995) for LEF mixed leaf litter after 120 days.

Percent K remaining showed highly significant species differences at all time periods (Table 1), and the species order of % K remaining (*Dacryodes* > *Miconia* > *Cecropia*) was maintained throughout the study period (Fig. 1b). Compared to other nutrients, little K remained after 16 weeks (10% for *Cecropia*), similar to other tropical

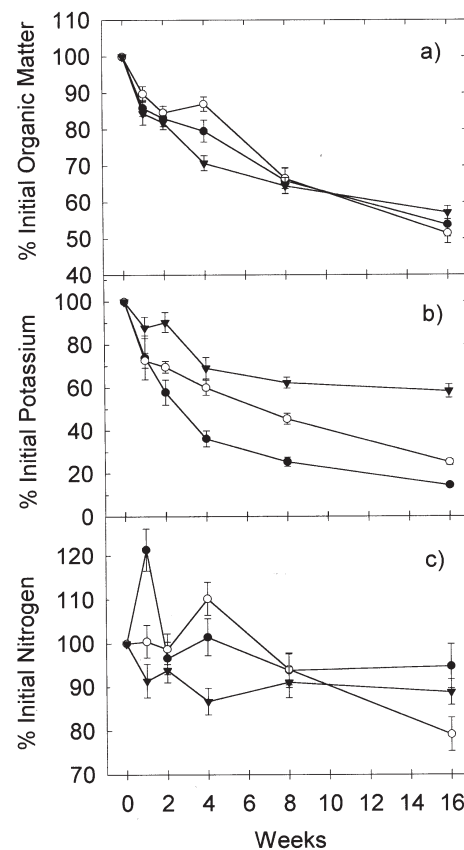


Figure 1. Mean and standard error ($n=12$) of chemicals remaining (percent) in all 36 litterbags at each of the five sampling periods grouped by species (a: initial organic matter), (b: initial potassium [K], c: initial nitrogen [N]). *Cecropia* is indicated by a filled circle, *Miconia* by an open circle and *Dacryodes* by a filled triangle.

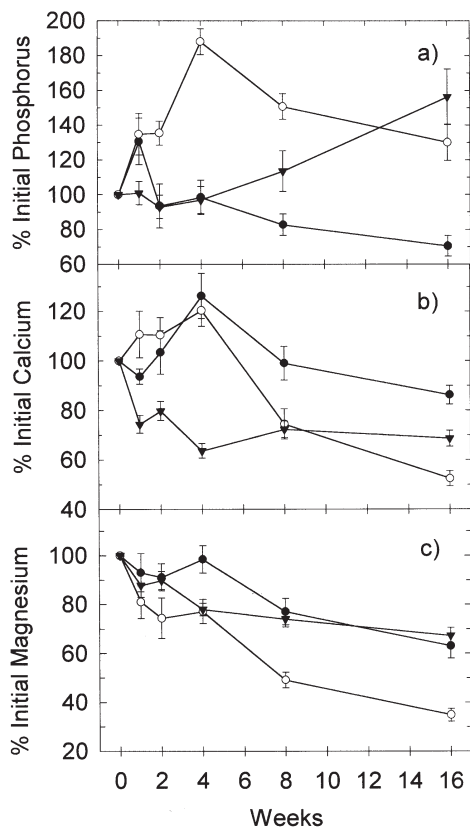


Figure 2. Mean and standard error ($n=12$) of chemicals remaining (percent) in all 36 litterbags at each of the five sampling periods grouped by species (**a**: initial phosphorus [P], **b**: initial calcium [Ca], **c**: initial magnesium [Mg]). *Cecropia* is indicated by a filled circle, *Miconia* by an open circle and *Dacryodes* by a filled triangle.

studies where K was released faster than other nutrients (Palm and Sanchez 1990, Zou et al. 1995). Both organic matter and K followed exponential decay without significant microsite differences (Table 1; Figs. 1ab).

Percent N remaining showed strong significant differences among species at all five time periods and marginal differences among microsites after 1 and 2 weeks (Table 1). Multiple-range testing indicated that the landslide border plots released N more slowly than the other microsites, but the Bonferroni test suggested that these results should be viewed with suspicion. *Cecropia* immobilized N after 1 week and *Miconia* immobilized it after 4 weeks. Later, N expressed as percent of the initial N was higher in *Cecropia* than in *Miconia* litterbags. *Dacryodes* also had small immobilization after 8 weeks. After 16 weeks, *Cecropia* was at 95%, *Dacryodes* at 90% and *Miconia* at 78% of initial N (Fig. 1c).

Percent P remaining showed significant species effects in each of the five sampling periods but no significant microsite effects (Table 1; Fig. 2a). There was P immobilization by all three species at different time periods: *Cecropia* immobilized P after 1 week, *Dacryodes* after 8 and 16 weeks and *Miconia* during all 5 time periods (Fig. 2a). P content of *Dacryodes* litter increased to 150% and *Miconia* to 180% after 4 weeks (Fig. 2a). Only N and P were immobilized by all three species. Both Ca and Mg had strong species effects at all time periods with no microsite effects (Table 1; Fig. 2bc). In addition, for Ca, there was immobilization for *Cecropia* (after 4 weeks) and *Miconia* after 1, 2 and 4 weeks (Fig. 2b).

Discussion

Mass loss of litter was very rapid in this tropical site, with nearly 50% loss within the first 16 weeks. Subsequent differences in mass loss among these species, is probably less likely than in the earlier stages. On the other hand, nutrient loss rates continued to show several strong interspecies effects at the conclusion of this study, and studies of longer duration should be able to shed additional light on those differences. Chemicals responded in an individualistic manner and dominance of species over environmental effects suggests that their interactions, had they been computed, could have been insignificant. Nitrogen and P immobilization are frequently reported in litter decomposition studies (Vitousek 1984), but Ca immobilization appears less common. Further, the absence of Ca immobilization in one species (*Dacryodes*) here argues against a soil contamination source. The high degree of P immobilization observed here for *Miconia* merits further study. This could be related to the unusually high initial leaf concentration of aluminum (22.1 g kg^{-1} vs. 0.82 in *Dacryodes* and 0.44 in *Cecropia*) in *Miconia*. This is surprising and we hypothesize that P immobilization in *Miconia* might occur by an abiotic mechanism analogous to geochemical immobilization. Lignin and polyphenol differences are often used to explain differences in decomposition rates (Palm and Rowland 1997). However, even if lignin and polyphenol differed among these species (which we did not measure), those differences did not result in different mass loss rates.

The N, P, and K results mirror the successional status of the three species: immobilization of N and P occurs first in *Cecropia* (early successional) then *Miconia* (middle) and finally, or not at all, in *Dacryodes* (late), and potassium loss is most rapid from *Cecropia* and slower in the other two species. Both N and P were immobilized in leaf litter bags containing these three species and in the same sequence as the species appear in succession. This is con-

sistent with the idea that nutrient immobilization by decomposing litter is most important during early succession when soil nutrients might be limiting plant growth. Where these species co-occur, this pattern could conserve these nutrients more effectively than in the absence of one or more species due to a greater variety of microbes being present.

While we cannot exclude the possibility that these patterns could have occurred by chance, that probability is 1 out of 6 (3 factorial) for each chemical and 1 out of 36 for both of them assuming they are independent events. The dominance of species effects suggests that other aspects of initial leaf litter chemistry could strongly influence decomposition. For example, N and P contents of leaves should lead to more rapid mass losses (Fogel and Cromack 1977), but we found no correspondence in our data to support those other findings.

Soil nutrient availability is a key ecosystem property, and Lugo (1992) and Silver (1994) suggest that levels of soil P, Ca and N are positively correlated with levels of the same nutrients in the litterfall, particularly for tropical montane forests like LEF. We found for N, but not for P, that there was a positive correspondence between litter and soil nutrient levels because both soil N (sampled in these same 12 microsites in 1992 and reported by Myster and Fernández [1995]), and litterfall flux multiplied by litter N concentration increase significantly from the forest to the center of the landslide. Finally, the result that plant species composition of the substrate accelerates or retards nutrient cycling to a greater extent than does the degree of environmental variation observed here, points to a soil decomposer biota acting similarly in the environmental ranges found in these landslide and forest microsites, but being more responsive to substrate quality.

In conclusion we found: (1) decomposition dynamics were the same in landslide and adjacent forest even though there were large environmental differences between the two sites, (2) the earliest-successional species examined here immobilized N and P most rapidly and to the greatest degree followed by the other two species in order of their successional status, consistent with the idea that nutrient immobilization by decomposing leaf litter is most important during early succession when nutrient uptake by roots is lowest due to low root density in the soil, and (3) *Miconia racemosa* litter both showed unusually high Al concentrations and immobilized the most P during decomposition of the three test species, which may be an important mechanism for P conservation in other ecosystems.

Acknowledgements: We first wish to thank Ligia Lebrón for her help in making the litterbags and in the organic matter and

nitrogen analysis. We also wish to thank the Analytical Laboratory, International Institute of Tropical Forestry, U.S. Department of Agriculture, for performing the other chemical analyses. Finally, we thank D. Zarin, D. J. Lodge and X. Zou for commenting on earlier versions of the manuscript. This research was performed under grants BSR-8811902 and DEB-9411973 from the National Science Foundation to the Institute for Tropical Ecosystem Studies, University of Puerto Rico and the USDA Forest Service International Institute of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support was provided by the Forest Service (U.S. Department of Agriculture) and the University of Puerto Rico.

References

- Brown, A. S. and A. E. Lugo. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14:161-187.
- Fernandez, D.S. and R. W. Myster. 1995. Temporal variation and frequency distribution of photosynthetic photon flux densities on landslides in Puerto Rico. *Tropical Ecology* 36:73- 87.
- Fogel, R. and K. Cromack. 1977. Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. *Canadian Journal of Botany* 55:632-1640.
- Guariguata, M.R. and M. C. Larsen. 1990. Preliminary map showing locations of landslides in El Yunque Quadrangle, Puerto Rico. *U.S. Geological Survey Open File Report* 89-257.
- Holdridge, L.R. 1967. *Life Zone Ecology*. Tropical Science Center, San Jose, Costa Rica. 206pp.
- La Caro, F. and R. L. Rudd. 1985. Leaf litter disappearance rates in Puerto Rican montane rain forest. *Biotropica* 17:269-276.
- Liu, Z. G. and X. M. Zou. 2002. Exotic earthworms accelerate plant litter decomposition in a tropical pasture and a wet forest. *Ecological Applications* 12:1406-1417.
- Lugo, A.E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. *Ecological Monographs* 62:1-41.
- Luh-Huang, C.Y. and E. E. Schultz. 1985. Digestion of plant tissue for analysis by ICP emission spectroscopy. *Communications of Soil Science and Plant Analysis* 16:943-958.
- Myster, R. W. 2002a. The use of productivity and decomposition to address functional redundancy in the Neotropics. *Community Ecology* 3:51-57.
- Myster, R. W. 2002b. Foliar pathogen and insect herbivore effects on two landslide tree species in Puerto Rico. *Forest Ecology and Management* 169:231-242.
- Myster, R.W. and D. S. Fernandez. 1995. Spatial gradients and patch structure on two Puerto Rican landslides. *Biotropica* 27:149-159.
- Myster, R.W. and L. R. Walker. 1997. Plant successional pathways on Puerto Rican landslides. *Journal of Tropical Ecology* 13:165-173.
- Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44:322-331.
- Palm, C.A. and P. A. Sanchez. 1990. Decomposition and nutrient release patterns of the leaves of three tropical legumes. *Biotropica* 22:330-338.
- Palm, C.A. and A. P. Rowland. 1997. A minimum dataset for characterization of plant quality for decomposition. In: Cadisch, G. and Giller, K.E. (eds.), *Driven by Nature: Plant Residue Quality and Decomposition*. CAB International, Wallingford, pp. 379-393.

- Rice, W.R. 1989. The sequential Bonferroni test. *Evolution* 43:223-225.
- SAS 1985. *User's Guide: Statistics*, Version 5. SAS Institute Inc. Cary, NC. 956 pp.
- Silver, W.L. 1994. Is nutrient availability related to plant nutrient use in humid tropical forests? *Oecologia* 98:336-343.
- Vitousek, P. 1984. Litterfall, nutrient cycling and nutrient limitation in tropical forests. *Ecology* 65:285-298.
- Vitousek, P. Gosz, J. R. Grier, C.C. Melillo, J.M. and W. A. Reiners. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecological Monographs* 52:155-177.
- Waedle, D.A. Bonner, K.I. and K. S. Nicholson. 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* 79:247-258.
- Weider, R.K. and G. E. Lang. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter-bags. *Ecology* 63:1636-1642.
- Zou, X. Zucca, C. P. Waide, R.B. and W. H. McDowell. 1995. Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. *Forest Ecology and Management* 78:147-157.