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## Bird perches and soil amendments as revegetation techniques for landslides in Puerto Rico

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BIRD PERCHES AND SOIL AMENDMENTS  
AS REVEGETATION TECHNIQUES FOR  
LANDSLIDES IN PUERTO RICO

by

Aaron Blakely Shiels

Bachelor of Science  
University of Denver  
1998

A thesis submitted in partial fulfillment  
of the requirements for

**Master of Science Degree  
Department of Biological Sciences  
College of Sciences**

**Graduate College  
University of Nevada, Las Vegas  
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Bird Perches and Soil Amendments as Revegetation Techniques

for Landslides in Puerto Rico.

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## ABSTRACT

### **Bird Perches and Soil Amendments as Revegetation Techniques for Landslides in Puerto Rico**

by

Aaron B. Shiels

Dr. Lawrence Walker, Examination Committee Chair  
Professor of Biology  
University of Nevada, Las Vegas

Landslides represent one of the most severe natural disturbances in tropical rainforests. The loss of the topsoil layer is detrimental to plant establishment and plant succession as it contains the soil seed bank, as well as the majority of the nutrients essential for plant growth. In this study, I introduced bird perches to six Puerto Rican landslides with three types of surfaces (bare, climbing fern, grass) to test the limitation of bird-dispersed forest seeds in landslides and to accelerate forest seedling establishment. I also mixed four soil amendments (*Cecropia* leaves, *Cyathea* fronds, forest soil, and commercial fertilizer) in five recent (<5 yr) landslides to determine soil and plant responses. Soils were sampled repeatedly over one year to measure soil chemical and physical properties, and I sowed seeds of two common landslide colonists (*Paspalum* and *Phytolacca*) to test the effects of these soil treatments on seed germination and seedling growth. This field experiment was also replicated under more controlled conditions in a screen-house experiment. Decomposition of *Cecropia* and *Cyathea* litter was also measured over 1 yr on the five landslides. The number of bird-dispersed forest seeds was

significantly higher beneath introduced perches compared to controls, and landslides with grass vegetation cover tended to have the most bird-dispersed forest seeds beneath perches compared to climbing fern and grass landslides. Perches did not increase forest seedling densities compared to controls. Seven different species of birds were observed on perches, and the majority of the bird-dispersed seeds were deposited below artificial perches at the time of greatest seed production in the forest (wet season). Because 99% of the seed inputs to landslides were wind-dispersed seeds (mostly graminoids), perches may improve landslide restoration in the long-term, but not the short-term (<14 mo), by attracting birds that bring in woody forest species. Once established, woody plants may overtop and shade out the dominant ground cover, thereby accelerating succession.

Commercial fertilizer increased plant-available soil nitrogen and phosphorus on landslides within 60 days, and also increased seed germination of *Paspalum* seeds when compared to soils treated with *Cecropia* leaves. Additionally, forest soil amendments increased total soil nitrogen and soil organic matter at 60 days. Despite these increases, there were no treatment differences with respect to seedling growth, perhaps because field treatment effects were overwhelmed by leaching and erosion. *Cyathea* litter decomposed more quickly than *Cecropia* litter on landslides, the latter retaining foliar nitrogen for 1 year. Neither *Cecropia* nor *Cyathea* facilitated seedling growth during 1 year. In the screen-house experiment, commercial fertilizer and forest soil treatments significantly increased seedling growth of both *Paspalum* and *Phytolacca*. Based on my experiments, commercial fertilizer and forest soil appear to be the best treatments for increasing soil fertility and plant growth in Puerto Rican landslides.



## TABLE OF CONTENTS

ABSTRACT.....	iii
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
ACKNOWLEDGMENTS.....	ix
CHAPTER 1    BIRD PERCHES INCREASE FOREST SEED INPUTS ON LANDSLIDES.....	1
Introduction.....	1
Materials and Methods.....	4
Study Site.....	4
Perch Additions.....	6
Bird Observations.....	7
Plant Succession Plots.....	9
Statistical Analysis.....	9
Results.....	11
Discussion.....	13
Conclusion.....	23
Tables.....	25
Figures.....	31
CHAPTER 2    RESPONSES OF SEEDS, SEEDLINGS, AND SOILS TO ORGANIC MATTER AND FERTILIZER ADDITIONS IN LANDSLIDES.....	38
Introduction.....	38
Materials and Methods.....	42
Study Site.....	42
Soil Amendments.....	44
Experimental Design.....	46
Field Soils.....	47
Decomposition.....	51
Screen-house Soils.....	52
Field Plant Responses.....	53
Screen-house Plant Responses.....	54
Statistical Analysis.....	55
Results.....	57
Soil Amendments.....	57
Field Soils.....	57

Decomposition .....	61
Screen-house Soils .....	62
Field Plant Responses .....	63
Screen-house Plant Responses .....	63
Discussion .....	65
Field Soils .....	65
Decomposition .....	71
Screen-house Soils .....	73
Field Plant Responses .....	75
Screen-house Plant Responses .....	79
Conclusion .....	81
Tables .....	84
Figures .....	94
APPENDIX .....	117
BIBLIOGRAPHY .....	121
VITA .....	134

## LIST OF TABLES

### CHAPTER 1

Table 1.1	Site characteristics for six landslides used for perch additions .....	25
Table 1.2	Seed species collected in perch and control plots.....	26
Table 1.3	Bird-dispersed and wind-dispersed seeds collected per m <sup>2</sup> .....	27
Table 1.4	Bird species observed on six landslides.....	28
Table 1.5	Bird visitation frequency to introduced perches .....	29
Table 1.6	MANOVA profile contrasts (time <sub>2</sub> -time <sub>1</sub> ) of percent ground cover ....	30

### CHAPTER 2

Table 2.1	Site characteristics for five landslides used for soil treatments .....	84
Table 2.2	Field available nitrogen MANOVA summary.....	85
Table 2.3	Field available nitrogen between subjects comparisons .....	86
Table 2.4	Field soil ammonium and nitrate concentrations.....	87
Table 2.5	Field soil variables MANOVA summary .....	88
Table 2.6	Field soil variables between subjects comparisons.....	89
Table 2.7	Field decomposition MANOVA summary .....	90
Table 2.8	Field decomposition foliar nutrient concentrations .....	91
Table 2.9	Screen-house <i>Paspalum</i> biomass and height MANOVA summary .....	92
Table 2.10	Screen-house <i>Phytolacca</i> biomass and height MANOVA summary ...	93

## LIST OF FIGURES

### CHAPTER 1

Figure 1.1	Schematic of seed baskets and succession plots.....	31
Figure 1.2	Seasonality of bird-dispersed seeds below perch and control plots ....	32
Figure 1.3	Bird-dispersed seeds (per m <sup>2</sup> ) below perch and control plots .....	33
Figure 1.4	Total number of bird species visiting perches during observations ....	34
Figure 1.5	Percent visitation of birds observed in four landslide locations.....	35
Figure 1.6	Average visitation time of birds observed on perches.....	36
Figure 1.7	Cover class frequency on three landslide cover types.....	37

### CHAPTER 2

Figure 2.1	Schematic of field soil treatment trays .....	94
Figure 2.2	Field soil nitrogen mineralization rate among treatments .....	95
Figure 2.3	Field soil nitrogen mineralization rate among landslides.....	96
Figure 2.4	Field soil ammonium among landslides.....	97
Figure 2.5	Field soil organic matter among treatments .....	98
Figure 2.6	Field soil nitrogen among treatments .....	99
Figure 2.7	Field soil available phosphorus among treatments.....	100
Figure 2.8	Field soil total phosphorus among treatments .....	101
Figure 2.9	Field soil pH among treatments.....	102
Figure 2.10	Field soil particle size among landslides .....	103
Figure 2.11	Decomposition among treatments .....	104
Figure 2.12	Decomposition among landslides at 60 d.....	105
Figure 2.13	Decomposition among landslides at 150 d.....	106
Figure 2.14	Foliar nitrogen of <i>Cecropia</i> and <i>Cyathea</i> among landslides.....	107
Figure 2.15	Screen-house soil variables .....	108
Figure 2.16	Percent <i>Paspalum</i> and <i>Phytolacca</i> seeds germinated in the field ....	109
Figure 2.17	Percent surviving <i>Paspalum</i> and <i>Phytolacca</i> seedlings in the field ..	110
Figure 2.18	Screen-house <i>Paspalum</i> seedling biomass .....	111
Figure 2.19	Screen-house <i>Phytolacca</i> seedling biomass .....	112
Figure 2.20	Screen-house <i>Paspalum</i> seedling height .....	113
Figure 2.21	Screen-house <i>Phytolacca</i> seedling height .....	114
Figure 2.22	Percent surviving seedlings in the screen-house .....	115
Figure 2.23	Conceptual model ranking field soils to soil fertility importance .....	116

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## CHAPTER 1

# BIRD PERCHES INCREASE FOREST SEED INPUTS ON LANDSLIDES

### Introduction

Landslides are among the most severe natural disturbances in tropical rainforests (Garwood et al., 1979; Walker et al., 1996; Myster & Walker, 1997; Restrepo & Vitousek, 2001), and are relatively common in Puerto Rico as a result of high rainfall events (e.g., hurricanes, tropical storms) and steep slopes (Larsen & Simon, 1993). Landslides cause loss of the topsoil layer of the soil profile (at least the O- and A-horizons) and loss of existing vegetation and the soil seed bank. This disturbance leaves bare scars on the landscape and initiates primary succession.

The availability of seeds has been proposed as one of the major limiting factors for plant colonization on landslides in Puerto Rico (Walker et al., 1996). Despite the importance of seed inputs to landslides, they have been rarely studied (although see Walker & Neris, 1993; Myster & Sarmiento, 1998), as the majority of past studies on seed dispersal into disturbed sites in the tropics have focused primarily on treefall gaps (Augspurger & Fanson, 1988; Denslow & Gomez Diaz, 1990) and land clearings (Young et al., 1987; Willson & Crome, 1989; Holl, 1998). Most landslides lack a significant seed bank (Guariguata, 1990), so plant succession depends primarily on seed rain (Restrepo &



Vitousek, 2001). Additionally, with the loss of existing vegetation following landslides, vertical structure is generally absent at early stages of landslide succession (Walker, 1994). Vertical structure is important for the attraction of vertebrate seed dispersers, such as birds and bats, that commonly disperse forest seeds in the tropics (Wunderle, 1997).

Wind dispersal often predominates over other types of seed dispersal in disturbed areas, as shown in forest gaps in Panama (Augspurger & Franson, 1988), and pastures in a dry forest in Costa Rica (Janzen, 1988). Small-sized seeds, such as those of grasses and ferns, may be the result of natural selection to enhance dispersal to germination sites (Baker, 1972; Jackson, 1981; Hoppes, 1988). Wind-dispersed species are often the first to colonize a disturbed site, physically and numerically dominating it for decades (Wunderle, 1997), as is the case for grasses and ferns on both Hawaiian (Restrepo & Vitousek, 2001) and Puerto Rican landslides (Walker, 1994; Walker & Boneta, 1995).

Vertebrate-dispersed seeds are more common than non-vertebrate-dispersed seeds in wet habitats (Wunderle, 1997). For example, in neotropical rainforests, vertebrate seed dispersal is common among 70-94% of woody plants (Howe & Smallwood, 1982; Jordano, 2000), but virtually absent or unimportant in grasslands (Jordano, 2000). Vertebrate dispersal is important to succession as frugivores affect plant demography and community composition by directing spatial distributions of seeds (Jordano, 2000). Most vertebrate-dispersers move large seeds that are common in mid- to late-successional forests (Wunderle, 1997).

Birds are often the major seed-dispersing vertebrate in tropical rainforests (Wunderle, 1997). This is the case in Puerto Rico where Devoe (1989) found the majority of animal dispersal in both forest understories and forest gaps was due to birds, rather than bats or

rodents. Although bats, rats, and mongoose also disperse seeds in the forests of Puerto Rico (Devoe, 1989; Willig & Gannon, 1996), the island lacks mammalian dispersers of forest seeds common to other rainforests in the Neotropics (Willig & Gannon, 1996), such as agoutis (Hallawachs, 1986) and primates (MacKinnon & MacKinnon, 1978). Therefore, increasing bird visitation to disturbed areas in Puerto Rico, such as landslides, will likely influence succession rates and trajectories.

Perch availability has been proposed as the primary factor influencing the number of bird-dispersed seedlings on an open site (Campbell et al., 1990). The likelihood of perches facilitating seed inputs generally increases in wet topical areas as vertebrate-dispersed seeds are more common than in drier regions (Wunderle, 1997). With the few tree saplings that could serve as possible perches in the early stages of landslide succession (Walker, 1994), facilitating the dispersal of forest seeds by birds into landslides by introducing perches could be an important method to promote forest seed input, seedling establishment, and forest recovery.

Although several studies have inferred that the presence of forest seeds and seedlings below established shrubs and isolated trees was a result of seed deposition by birds (Guevara, 1986; Toh et al., 1999; Slocum, 2001), experimental studies using introduced perches as recruitment foci have been less commonly studied, especially in tropical regions. Introduced bird perches have been constructed to increase seed rain in pastures within temperate regions (McDonnell & Stile, 1983; McDonnell, 1986), temperate mined sites (McClanahan & Wolfe, 1993), and tropical pastures in Costa Rica (Holl, 1998) and Colombia (Aide & Cavelier, 1994). The general findings of these studies indicate that seed rain beneath perches in pastures is significantly greater than non-perch areas within

the pasture (McDonnell, 1986; Holl, 1998). These same studies show that the types of seeds dispersed beneath the perches were highly variable, including seeds from the pasture, forest edge, and mature forest. Although seedling establishment was not compared in the majority of these studies, Holl (1998) did not find any difference in the number of bird-dispersed seedlings beneath perches and controls after 19 months, and McClanahan and Wolfe (1993) found a minor increase in bird-dispersed seeds below perches after 6 years.

In this study, perches were added to landslides in Puerto Rico to determine the ecological role of birds in contribution to succession on landslides, as well as to test the practicality of perches to increase forest seed inputs and increase forest recovery on landslides. Because landslides are generally at different stages of succession with different ground cover characteristics, bird visitation and seedling establishment may also be different. Therefore, I picked landslides dominated by grasses, climbing ferns, or bare soil and addressed whether perch additions increased the density of bird-dispersed seeds and seedlings of forest species compared to landslide areas without perches. I also examined whether ground cover on landslides affected perch visitation and forest seedling establishment.

## Materials and Methods

### Study Site

This study took place on landslides between 450-650 m a.s.l. in the Luquillo Experimental Forest (LEF). The LEF covers roughly 110 km<sup>2</sup> (11,000 ha) in northeastern Puerto Rico, between 18° 15'N-18° 23'N and 65° 52'W-65° 48'W.

Mean annual precipitation ranges from 3000-4000 mm with high year-to-year variation and little seasonality. Mean monthly temperatures range from 21-25°C (Brown et al., 1983; Soil Survey Staff, 1995). The natural vegetation in the study area is subtropical lower montane wet and rain forest *sensu* Holdridge (Ewel & Whitmore, 1973). Landslide vegetation is dominated by high-light tolerant species typical of early succession. Common landslide-colonizing vegetation includes several types of grasses (e.g., *Andropogon*, *Paspalum*), ferns (e.g., *Cyathea*, *Nephrolepis*, *Dicranopteris*, *Gleichenia*), and herbs (e.g., *Nepsera*, *Sauvagesia*), as well as woody colonizers, such as *Cecropia* and *Tabebuia* (Walker & Boneta, 1995; Walker et al., 1996). Botanical nomenclature follows Little et al. (1974) for trees, Taylor (1994) for other flowering plants, and Proctor (1989) for ferns.

There are 246 bird species occurring on the island of Puerto Rico, of which approximately half are breeding permanent residents and half are non-breeding migrants and visitors (Raffaele, 1989). The LEF is home to 66 species of land birds (Wiley & Bauer, 1985). Several species are found more frequently in forest gaps than in the mature forest (Wunderle et al., 1987). Over the elevational range covered by the chosen landslides, avian species diversity was similar (J. Wunderle, personal communication).

Six landslides in the LEF were chosen for artificial bird perch additions. Landslides in the LEF usually occur after high rainfall events, often associated with hurricanes and tropical storms. In this study, like that of Guariguata (1990), a landslide was defined as an area where shear strain and displacement of a mass of ground creates a defined surface of rupture (Varnes, 1978). Landslides <20 m wide or long were excluded from this study. From all remaining landslides in the LEF that were readily accessible (i.e., <200

m from a road), I randomly chose two landslides from those dominated by each of the following three vegetation types: Gleicheniaceae climbing fern (ES9, ES17), grass (ES15, ES16), and bare (>80% exposed soil; RB12, MY7). Landslides were defined by watersheds (Río Espiritu Santo=ES, Río Blanco=RB, and Río Mameyes=MY, and numbers used in other landslide studies).

#### Perch Additions

Bird perches (hereafter referred to as perches) were erected on each of the six landslides. On each landslide, I established four circular plots (each 2 m in diameter;  $3.14 \text{ m}^2$ ) no closer than 5 m from the nearest forest edge to the center of each plot, such that each plot was  $\geq 4$  m on center from each adjacent plot. Plots were arranged as one of four corners of a square or along a straight line following the forest edge, depending on the landslide dimensions. Two of the four plots on each landslide were randomly assigned perches and two plots served as controls. Perches were made from small trees retrieved near each landslide, stripped of leaves, flowers, and fruits, and erected to a height of 4-4.5 m above the ground. Perches were held in place by burying *ca* 0.7 m of the lower section of the perch in the ground and stabilizing the perch by attaching guide wires to stakes. All perches were thinned to have approximately equal branching area (17-18 branches >1 cm diameter at the main stem). Naturally growing tree saplings or large shrubs >1.3 m tall within 5 m of each plot were cut down in order to reduce their influence on perch visitation. On climbing fern-covered landslides (ES9, ES17), all perch and control plots were trampled equally at the onset of the experiment to account for vegetation damage caused by erecting the perches.

Within each perch and each control plot, ten 33 x 23.5 cm subplots (each 0.0776 m<sup>2</sup>) were haphazardly located at least 10 cm from each other. Subplots were randomly assigned to either trap seeds or record short-term successional changes in vegetation (described below). Five seed baskets were placed on the ground surface in each plot (Fig. 1.1), secured with a 30 cm stake, lined with nylon cloth (3 threads mm<sup>-1</sup>) to trap seeds, and finally covered with 1.3 cm metal screening to keep out rodents. Seed traps were visited every 3 weeks between 14 June 2000 and 17 August 2001. Pieces of nylon cloth were exchanged upon seed collection with clean cloths of equal size. Once seeds were collected, they were identified to species using matching seed samples collected from the surrounding forest and landslides. Only diaspores  $\geq 2$  mm long were counted and identified and each seed was categorized as bird-dispersed or wind-dispersed based on seed size, morphology, and reference to Devoe (1989). Wind-dispersed seeds included not only those dispersed strictly by wind, but also those dispersed by gravity and one species dispersed by epizoochory (*Desmodium*). Due to the high quantity of <1 mm seeds in *Miconia* (Melastomaceae) fruits, the fruits collected from species in this family were counted as a single bird-dispersed seed if found >50% intact.

Dominant vegetation surrounding each landslide was noted, and elevation, area, aspect, slope, and light were also recorded for each landslide (Table 1.1).

#### Bird Observations

I conducted bird observations from 1 June 2001 to 15 August 2001 in the LEF on the six landslides that were used for perch additions. Bird observations took place from either 5:30-8:00 or 12:00-2:00 pm. The morning observation period was used as the main sampling period because it represented the time period of most bird activity in this

forest (J. Wunderle, personal communication; A. Shiels, personal observation).

However, less frequent mid-day sampling was conducted at these sites in order to account for potential species and/or visitation differences from morning to afternoon. Avian identification was based on Raffaele (1989).

Two randomly chosen landslides were visited during each sampling day. The total time of observation at each landslide was 1 hr for the morning sampling and 0.5 hr for the afternoon sampling. A conservative sampling approach was taken in order to account for potential variation between the dawn hour and the second hour by sampling all landslides evenly across the entire sampling period (i.e., June-August, at dawn and second hour). During each observation period, I was stationary, partially concealed by surrounding vegetation, at a distance of 5-8 m from the nearest introduced perch. This position allowed me to be able to see 360 degrees, as well as to clearly see both perches. Weather conditions at the time of each observation were noted. For each bird observation, the bird species (only family for most Columbidae), the locations in which birds were observed, and the total visitation time within the respective location, was recorded. The four location categories included: on the perch, in the landslide on a natural perch, on vegetation at the forest edge (i.e.,  $\leq 15$  m into the forest), or flying over the landslide without perching in landslides or at the forest edge. Care was taken to account for individuals that may have been counted twice. However, the quantity of time birds spent in the landslide area was the primary focus of these observations rather than the number of individuals.

Although seasonality was not accounted for in this bird observation study, the single, three-month period of bird observation is likely to be representative, or an underestimate,

of mean daily bird visitation given that all the birds observed were classified as non-migratory (Raffaele, 1989). Additionally, past mist-capture studies suggest that the bird populations for this area do not change seasonally except when a hurricane during the previous year disrupts bird activities (Waide, 1991).

#### Plant Succession Plots

Short-term plant succession subplots were delineated in perch and control plots to compare the establishment of bird-dispersed vegetation over the 14 mo perch-addition experiment. Each of the five plant succession subplots, matching dimensions of the seed baskets, was visited in July 2000, August 2000, January 2001, June 2001, and August 2001. Subplots were not weeded at any point during the experiment. During each visit, I used five cover classes (0 - 0%, 1 - 1-15%, 2 - 16-30%, 3 - 31-50%, 4 - 51-75%, 5 - 76-100%) to determine percent cover of litter, bare soil, graminoids, ferns, and shrubs+herbs. Shrubs (e.g., *Miconia*, *Palicourea*, *Psychotria*) were combined with herbs due to their small (<12 cm) size and herbaceous morphology as seedlings. Vegetation used for cover measurements was rooted within subplots, and plants in each life form were identified to species and recorded. In order to determine if vegetation changes occurred during the experiment, the July 2000 period ( $\leq 45$  days after perch addition) was used as a standard comparison for all subsequent vegetation measurements.

#### Statistical Analyses

The average of bird-dispersed seed totals caught at the end of the experiment below perches and controls at each landslide was compared using a Wilcoxon rank scores test ( $n=6$  for each perch and control). The average of bird-dispersed seed totals below perches were then compared among the three landslides cover classes (bare, climbing



fern, grass) using a Kruskal-Wallis test. The total number of wind-dispersed seeds at each of the four plots within a landslide were first averaged to compare landslide cover classes using a Kruskal-Wallis test. However, it should be noted that sample sizes for each of the cover classes were small ( $n=2$  for each). Frequency of visitation to perches for each observation period was similarly compared among landslides, and among cover class types using Kruskal-Wallis tests. Durations of bird visitation to perches was compared among landslides and among cover classes using one-way ANOVAs after homogeneous distributions were determined (two-way ANOVAs could not be used because of lack of replication on one landslide). The number of bird-dispersed plants (defined in Devoe, 1989) below perches and controls were compared using a Wilcoxon rank scores test ( $n = 6$  for each perch and each control). All statistical analyses described above were performed using JMP (2000), significance was determined at  $P<0.05$ , and means are presented  $\pm 1$  SE.

Vegetation cover class data, were analyzed by comparing plot means of midpoints of each cover class with a doubly-multivariate repeated-measures MANOVA using SAS (SAS Institute, 1996). Means were transformed to arcsine-square roots prior to analysis. Perch and control plots were combined for analysis such that bare, fern-, and grass-covered landslides each had eight plot comparisons. Significance was determined at  $P<0.05$ . Following this analysis, contrasts were used to compare variable changes through time (SAS Institute, 1996). Means were evaluated to determine which landslide type(s) contributed most to the differences supported in the contrasts; however, means for each comparison (landslide type vs. time vs. variable) were not compared statistically due

to the small sample size, the large number of comparisons necessary, and the high probability of making a Type I error.

## Results

A total of 21,507 seeds ( $\geq 2\text{mm}$ ) were collected on the six landslides during the 14-month study. Approximately 1%, or 222 seeds, were classified as bird-dispersed, and the majority of these (89 seeds) were *Schefflera morototoni*. The majority of wind-dispersed seeds were from two types of grasses, *Paspalum conjugatum* and *Andropogon bicornis* (Table 1.2). Inputs of bird-dispersed seeds changed seasonally, with most seeds appearing from April to September in both years of the study (Fig. 1.2).

When averaged across all six landslides, perch plots had significantly more bird-dispersed seeds than control plots ( $\chi^2=7.79$ ;  $df=1$ ;  $n=6$  sites;  $P=0.005$ ; Fig. 1.3). Over the course of the 14 mo study, only two bird-dispersed seeds were found in the control plots within all six landslides. Perches increased seed species richness as 14 of the 28 total species collected were bird-dispersed and only found in perch plots, whereas 12 species were wind-dispersed and found in both perch and control plots. However, variation among landslides was high with respect to species richness (Table 1.2).

Although not statistically significant ( $\chi^2=3.43$ ;  $df=2$ ;  $P=0.18$ ), landslides with grass-dominated ground cover tended to have more bird-dispersed seeds below the perches compared to both climbing fern-covered landslides and bare landslides (Table 1.3). Additionally, landslides varied widely with respect to wind-dispersed seeds, with the highest number of wind-dispersed seeds from RB12 (Table 1.3), but with no significant difference among vegetation cover types ( $\chi^2=3.43$ ;  $df=2$ ;  $P=0.18$ ).

Twenty-two species of birds were identified on the six landslides during the bird observation portion of the study. Bananaquits, Black-faced Grassquits, Puerto Rican Emeralds (hummingbirds), and Scaly-napped Pigeons were found at all six of the landslides. Seven of the 22 bird species were observed on the perches (Table 1.4).

During the 30 hours of total bird observation at the six landslides, an average of 1.50 birds visited perches per hour, and morning observations of birds on perches (1.46 bird hour<sup>-1</sup>) were similar to afternoon observations (1.67 birds hour<sup>-1</sup>). The average number of visitations to perches was not significantly different among landslides ( $\chi^2=6.64$ ;  $df=5$ ;  $P=0.25$ ) or vegetation cover types ( $\chi^2=4.45$ ;  $df=2$ ;  $P=0.10$ ). Bare landslides tended to have the lowest bird visitation to perches (Table 1.5).

The total number of bird species visiting perches varied among landslides, but overall, ES16, a grass-dominated landslide, had the highest number of bird visitations to perches (Fig. 1.4). Black-faced Grassquits were the most common visitors to perches at four of the six landslides, Puerto Rican Tanagers were the only birds observed on perches at the fern-covered landslide ES9, and a single Stripe-headed Tanager was the only observed visitor to perches on the bare landslide MY7 (Fig. 1.4).

When the four locations of bird observations were compared on (introduced) perches, on natural perches, on vegetation at the forest edge, or flying over the landslide, birds were most commonly observed perching at the forest edges for all six landslides (Fig. 1.5). Birds frequented both artificial and natural perches within landslide ES9 more than any other landslide. The average time birds occupied perches was  $1.10 \pm 0.30$  minutes per visit. The average visitation time on perches was not different among landslides ( $F=2.09$ ;  $df=5$ ;  $P=0.09$ ) or cover types ( $F=0.67$ ;  $df=2$ ;  $P=0.52$ ). Puerto Rican Tanagers on

landslide ES9, and Gray Kingbirds on the grass-covered landslide ES15 were the two species with the longest duration on the perches (Fig. 1.6).

Cover values across all landslides (grass, climbing fern, bare) changed significantly over the 14 mo period ( $P < 0.003$ ; Table 1.6). Mean bare, fern, and shrub+herb cover changed at different rates with respect to landslide type ( $P < 0.03$ ; Table 1.6). Grass-dominated landslides changed the least, as only bare soil cover decreased (Fig. 1.7). Climbing fern-dominated landslides increased in fern vegetation and shrubs+herbs cover. Bare landslides had the greatest decrease in bare soil cover, and increased in shrub+herb cover. Litter and graminoid cover both increased over time when averaged across all landslides ( $P < 0.003$ ), but differences among landslides were not significant (Table 1.6).

The presence of bird-dispersed plants that colonized the six landslides was low overall, ranging from  $1.49 \pm 1.26$  individuals  $m^{-2}$  in control plots to  $5.15 \pm 2.10$  individuals  $m^{-2}$  in perch plots after the 14 mo study. Despite the tendency toward a slightly higher number of bird-dispersed plants beneath perches, there were no significant differences between bird-dispersed plant species below perches and controls across all landslides ( $\chi^2 = 1.87$ ;  $df = 1$ ;  $P = 0.1715$ ).

## Discussion

Bird perches increased the amount of bird-dispersed seeds found on six landslides in the Luquillo Experimental Forest. The bird-dispersed seeds were tree and shrub species commonly found in mid- to late-successional forests in the LEF. Only two bird-dispersed seeds were found in control plots without perches during the 14 mo study. The majority of unaided seed inputs to these landslides were of wind-dispersed, early successional

species. Seven species of birds were observed using introduced perches during the study. Therefore, adding perches increased bird visitation and accelerated the accumulation of avian-dispersed forest seeds on landslides. Over the long-term, perches thus create the possibility of accelerating forest regeneration on landslides in the LEF.

Perches increased seed species richness on landslides, as 14 different species of seeds (all bird-dispersed) were found under perches that were not found in control plots. This result is similar to Holl (1998) where 14 different species of seeds were found beneath perches, although more than half of those likely dispersed from the remnant trees in the pasture and not the adjacent forest. The doubling of seed species richness by perch addition across the six landslides reinforces the observation that forest seeds are unlikely to occur on landslides when perches are absent.

Seasonality appears to be important for inputs of bird-dispersed seeds beneath perches in landslides, as they accumulated during the wetter part of the year in the LEF, from April through September. Two possible explanations for this include synchrony with fruiting in the forest and increased bird activity. The former is supported in this study by fruiting phenology data obtained in LEF from 1997-1998 (J. Zimmerman, unpublished data) correlating with peak dispersal of forest seeds below artificial perches. Most notable was the increase in *Schefflera* seeds below perches (40% of total bird-dispersed seeds) which showed peak seed deposition in both the forest and below perches from March to August. I also noted nesting of bird species that were observed on the perches during the period of highest seed dispersal. Therefore, both possibilities support the seasonal increase of bird-dispersed seeds, a pattern also noted in Panama (Foster, 1982), Costa Rica (Levey, 1988), and Brazil (Jackson, 1981).

Traps under perches with grass-covered understories tended to have more seeds than perches with bare soil or climbing fern understories, although a larger sample size is needed to robustly test this hypothesis. Attraction of birds to perches in the two grass-covered landslides may result from the vegetated ground providing more cover or a better source of food than bare ground (Wunderle, 1997). Interestingly, the majority of positive effects of perches have been found in pastures (McDonnell & Stiles, 1983; McDonnell, 1986; Holl, 1998). To date, only one perch study has shown positive effects with a bare understory (McClanahan & Wolfe, 1993). In addition, perches with climbing fern understories were functionally less elevated from the understory because the climbing ferns often reached heights of >1.5 m while the grasses were more sparse and <1 m tall. Taller perches promote bird visitation (J. Wunderle, personal communication), and this was demonstrated with both natural and artificial perches in past studies (McDonnell, 1986; Toh et al., 1999). Another possibility for the increase in bird-dispersed seeds under perches on the two grass-covered landslides is the presence of Gray Kingbird nests at the base of both of those landslides (personal observation). Gray Kingbirds are often found perched on telephone wires along roadsides (Raffaele, 1989; personal observation), as was the case in this study. The grass cover may still have been critical as there are telephone poles and wires near all landslides, yet the Gray Kingbirds were only found nesting adjacent to the grass-covered landslides.

Without perches, a total of 14 seed species were trapped (12 wind-dispersed + 2 bird-dispersed) during the study, which was low compared to total species trapped in two landslides after Hurricane Hugo (22 species; Walker & Neris, 1993), and in treefall gaps in LEF (49 species; Devoe, 1989). The difference in landslide species richness could in

part be due to the greater distance from the forest edge ( $\geq 5$  m) in this study compared to Walker and Neris ( $\geq 2$  m).

Seed rain in this study was high compared to previous studies of disturbed sites in the tropics. When wind-dispersed seeds were compared on a daily basis, seeds trapped ranged from 11.1 (bare), 5.5 (grass), and 0.1 (climbing fern) seeds  $\text{m}^2 \text{day}^{-1}$ . The bare and grass habitat variables were higher than seed dispersal (combined wind- and animal-dispersed) into lowland rainforest tree-fall gaps in Costa Rica (1.6 seeds  $\text{m}^2 \text{day}^{-1}$ ; Denslow & Gomez, 1990), gaps in the LEF (0.78 seeds  $\text{m}^2 \text{day}^{-1}$ ; Devoe, 1989), and forest understory in the LEF (2.55 seeds  $\text{m}^2 \text{day}^{-1}$ ; Devoe, 1989). This suggests that bare and grass-covered landslides have higher seed inputs than forests and forest gaps in the LEF. Although graminoid seeds were not considered, open landslides in the LEF trapped 0.3-1.8 seeds  $\text{m}^2 \text{day}^{-1}$  (Walker & Neris, 1993). Approximately 99% of all seeds collected in the six landslides were of wind-dispersed, early-successional vegetation types and 96% of those early-succession species were graminoids. LEF landslides are often rapidly colonized by grasses that can persist and dominate for decades (Walker, 1994; Walker & Boneta, 1995). Therefore, without perching structures, seed inputs from this study suggest wind-dispersed graminoids and herbs will colonize and persist on grass-covered and bare landslides.

Although the intact forest was not compared to landslides, the majority of the birds observed were at the forest edge, and species richness within the landslide habitat (which included the forest edge to  $\leq 15$  m) was higher (22 total species) than a previous report of mist-net captures in gaps, forest openings, and the forest understory in Puerto Rico (17 total species; Wunderle et al., 1987). This agrees with a past study in the tropics that

showed bird species richness is higher in forest gaps than intact forests (Schemske & Brokaw, 1981).

Birds frequented the perches more often (*ca* 1.5 visits hour<sup>-1</sup>), but stayed perched a shorter duration in this study (*ca* 1.10 minutes) when compared to a perch study in a Costa Rican pasture (*ca* 0.12-0.41 visits hour<sup>-1</sup>; *ca* 3.2 minutes; Holl, 1998). The difference between studies may be explained by variation in the distance to the forest edge, as perches were much further from the forest edge in Holl (25-250 m) compared to those in my study (5 m). Additionally, the majority of the birds in Holl were common to the pasture (7 out of 10) and not to the forest, whereas my study had 3 out of 7 bird species (Black-faced Grassquits, Yellow-faced Grassquits, Gray Kingbird) restricted to open areas and not the forest. Therefore, bird species composition and proximity of perches to the forest edge may influence bird visitation to perches, and both of these attributes may affect forest seed dispersal into disturbed areas.

Bird defecation at perches is likely to correlate with perch visitation and duration. Murray (1988) has suggested, from radio-tracking in Costa Rica, that birds spend between 7-12 minutes in one location, presumably consuming fruit, followed by perching nearly motionless for *ca* 10 minutes before moving on in search of more fruit. Seed passage rates vary, as regurgitation of seeds is rapid, from 5-20 minutes, whereas seed passage through defecation can be longer, ranging from 0.3-1.5 hours (Murray, 1988; Jordano, 2000). Birds were not observed to defecate while on perches in this study as they were on two occasions in the study by Holl (1998). However, excrement (uric acid) was noted multiple times on seed baskets and ground cover below perches throughout the experiment. Despite this evidence, regurgitation appeared to be the most-common form



of large seed dispersal as uric acid was not present when seeds were retrieved from seed baskets, and many of the bird species in this forest have been commonly noted regurgitating seeds (J. Wunderle, personal communication). Therefore, more frequent visits and longer stays at perches are suggestive of increased defecation below perches in vegetated landslides, and the larger seeds present beneath the perches suggest that most of the bird-dispersed seeds were likely regurgitated rather than passed through the digestive tract.

Although avian dispersers include both birds and bats, perching by bats on the perches used in this study was unlikely. There is only one species of frugivorous bat that frequents the forest understory at this elevation in the LEF and it prefers larger perches than those used in this study (M. Gannon, personal communication). Only two species of the seeds present beneath the perches (*Clusia clusioides* and *Clusia rosea*) have been documented as being bat-dispersed (Willig & Gannon, 1996; M. Gannon, personal communication). There was no evidence of bat excrement below perches, and past observations by several individuals in the LEF (see Devoe, 1989) determined that birds, not bats, take the majority of seed species similar to those found below the perches.

Most of the bird species observed are considered at least facultatively omnivorous, consuming seeds, fruits, and insects (Waide, 1991; Waide, 1996) and are capable of dispersing forest seeds onto the landslide or landslide edges. Gray Kingbirds, observed at four, and Puerto Rican Tanagers, observed at all six landslides, were the two species that occupied perches for the longest duration of the seven species observed on the perches. Puerto Rican Tanagers, classified as omnivores, have been noted consuming fruits from species in the Rubiaceae such as *Palicourea* and *Psychotria* (Waide, 1996). These seeds

were represented in the seed traps at two and three of the six landslides, respectively.

Gray Kingbirds are in the flycatcher family but have been known to regularly consume fruits (A. Shiels, personal observation; R. Waide, personal communication). Both species likely dispersed forest seeds to perches based on visitation frequency and duration, as well as their larger gape widths compared to most other species observed on perches. Gape sizes of birds usually correlate with fruit and seed sizes they are capable of dispersing (Jordano, 2000), and many of the seeds dispersed below the perches were larger than 0.5 cm in length (e.g., *Guarea*, *Matayba*, *Myrsine*, *Nectandra*, *Rourea*, *Roystonea*). In particular, Puerto Rican Tanagers were common on both perches and natural perches within the ES9 landslide, perhaps suggesting that a higher quantity of perches are more attractive to birds as visiting foci.

Although Black-faced Grassquits were the most frequent visitors to perches on almost all of the landslides, it is unlikely that this species, or the Yellow-faced Grassquits, dispersed forest seeds below perches because they have mostly granivorous diets, feeding primarily on seeds of grasses and sedges (Wetmore, 1916; Waide, 1996). Similarly, Puerto Rican Emerald hummingbirds are nectivores, consuming nectar and insects, and are unlikely to be dispersing forest seeds. Bananaquits, the most common bird species in the local area of the LEF (Waide, 1996), are also classified as nectivores and frequented all the landslides. This species may be capable of dispersing small-sized seeds, as field observations from the LEF and other islands in the Caribbean suggest that fruit, nectar, and invertebrates are common to a Bananaquit's diet (Snow & Snow, 1971; Waide, 1996). Judging by the Bananaquit's small gape size, many of the seeds collected below

the perches would be too large for Bananaquits to disperse, but seeds such as those from *Clusia clusioides*, *Miconia*, and *Passiflora* might be dispersed by Bananaquits.

Despite an increase in bird-dispersed seeds below perches compared to control plots, there was no difference in the presence of bird-dispersed seedlings when perch plots and control plots were compared. This result is similar to that found in Holl (1998). Other previous artificial perch studies did not address this issue (McDonnell & Stiles, 1983; McDonnell, 1986; Aide & Cavelier, 1994) or found only a slight increases in the number of bird-dispersed seedlings below perches compared to controls after 6 years (McClanahan & Wolfe, 1993). There are several factors that could have influenced this absence of more bird-dispersed seedlings below landslide perches, including: consumption of seeds by predators, seed loss due to steep landslide slopes and erosion, insufficient soil nutrients or unfavorable microclimate, and too short a time period to detect changes in bird-dispersed plant succession.

Rat (*Rattus* spp.) activity was noted in both perch and control plots as rat feces were present on a monthly basis on the tops of the metal screenings covering the seed baskets as well as inside the seed baskets. Although this may not have affected the number of bird-dispersed seeds trapped in the seed traps due to the wire-mesh coverings over the traps, it likely contributed to loss of bird-dispersed seeds in the remaining areas of the plots. In addition to rats, ants may have also contributed to potential seed loss from the succession plots. Although ant predation of seeds in landslides in the LEF was proposed to be minimal by Myster (1997), I observed ants taking seeds of *Clusia rosea* on one occasion from the seed baskets below a bird perch. Ant predation of bird-dispersed seeds

likely had less of an influence than rat predation given that most of the bird-dispersed seeds were large (>0.5 cm long).

Loss of seeds due to erosion or overland flow was more likely on bare landslides than on climbing fern- or grass-covered landslides where vegetation and litter might reduce run-off and trap seeds. Soil nutrient concentrations are low overall on landslides in the LEF (Guariguata, 1990; Walker et al., 1996). Although it is rare for most seeds to require nutrients to germinate, the landslide microclimate is severe (Walker, 1994; Everham et al., 1996; Walker et al., 1996) and survivorship to germination and seedling establishment is generally low. When *Phytolacca* seeds were sown in landslides in the LEF, there was 100% mortality after 8 months (see Chapter 2). Therefore, forest seeds deposited below perches may not have survived due to the harsh microclimate and infertile soils.

The final, and most probable cause of the lack of increased forest seedling densities below perches is the short duration of this study. This result is supported by past artificial perch studies conducted over a remarkably short time period (19 months: Holl, 1998; 14 months: this study) to show changes in plant succession. Moreover, the single study showing evidence of successional changes due to perches demonstrated only a slight increase (1.4-2.0 plants m<sup>-2</sup> below perches vs. 0-0.7 plants m<sup>-2</sup> below controls) after six years in forest seedlings dispersed by birds (McClanahan & Wolfe, 1993). Succession to pre-disturbance forest biomass on bare-surface landslides in the LEF is estimated to take up to 500 yr, although succession on landslides with existing topsoil may be as short as 50 yr (Walker et al., 1996).

Despite the minimal effect of bird-dispersed seeds on vegetation changes over the 14 mo time period, there were vegetation changes not attributed to bird dispersal. The most pronounced cover change occurred on the bare landslides, shown by the greatest decrease in bare soil, and greatest increase in shrubs+herbs compared to all other cover variables measured. Based on the high graminoid seed inputs recorded for RB12, it was surprising that there was not a substantial increase in graminoid cover for the bare landslides. However, this could be a result of secondary erosion, which is common on recent, minimally vegetated landslides (Walker et al., 1996). The high values of bare soil in succession plots on climbing fern-covered landslides were likely a result of the trampling of the canopy in each plot when the experiment began. Once the canopy was trampled, the deep and prominent litter layer characteristic of the Gleicheniaceae growing on landslides in the LEF (Walker, 1994; Fig. 1.7) was likely partially washed away exposing the bare soil. However, Gleicheniaceae commonly recovers quickly following disturbance, as shown when climbing fern-covered landslides were burned (Walker & Boneta, 1995) and in this study as fern and shrub+herb vegetation cover increased on climbing fern-covered landslides during the 1 yr period. Lastly, plant succession changed minimally on grass-covered landslides, as only bare-soil cover decreased.

Landslides in this study are clearly at different stages of succession. Despite the higher cover on climbing fern- and grass-covered landslides, the rate of plant succession may be attenuated due to the low diversity of vegetation life-form composition. Monotypic stands of both climbing fern and grasses are common on landslides in the LEF, and succession trajectories are slowed as a result (Walker, 1994; Walker & Boneta, 1995). For this reason, influencing successional trajectories may be most successful on

recent landslides that have minimal vegetation colonization (i.e., bare landslides) as suggested in the study by Restrepo and Vitousek (2001). *Tabebuia* tree seedling establishment below climbing ferns is inhibited by deep shade (Walker, 1994). However, *Tabebuia* seeds, an early successional tree, were found in traps at control plots in all six landslides. If able to germinate and establish, this wind-dispersed species can shade out grasses and ferns as well as facilitate bird-dispersed seeds (Walker, 1994). Grasses can also inhibit establishment of seeds in pastures (Holl, 1998) especially when densely clumped making it difficult for seeds to reach the soil (Nepstad et al., 1990; Restrepo & Vitousek, 2001). However, Aide and Cavelier (1994) found seeds germinated better in sparse pasture grasses (more similar to the grasses on landslides in Puerto Rico), which they believed was due to the positive effect of grasses on the microclimate. Bare landslides in this study had the most light and the most open patches of bare ground where germination would be likely, especially for species such as *Guarea* and *Schefflera* which have been shown to germinate better in high light environments (Everham et al., 1996).

### Conclusion

Additions of perches increased numbers of bird-dispersed seeds that are of mid- to late-successional origin in the LEF. Although I did not observe comparable increases in establishment of forest plant species, this was likely the result of insufficient time for a difference to be detected, or possibly due to seed loss from predation, erosion, low nutrients, or severe microclimate. Nevertheless, perch additions to landslides create the possibility of accelerating the accumulation of a forest seed bank. Whereas the majority

of seed inputs to landslides in the LEF are wind-dispersed graminoids that commonly colonize and dominate vegetation along with climbing ferns of the family Gleicheniaceae, the need for forest seed inputs to accelerate forest regeneration in landslides becomes crucial. It is uncommon for any significant perching structures to establish before grasses and ferns colonize landslides, and seedling survival and growth of forest seedlings beneath the canopy of Gleicheniaceae is difficult (Walker, 1994). Additionally, birds, which are the primary dispersers of the majority of the woody forest species in the LEF, seem to favor perches on landslides with some vegetation ground cover (mainly grass). Therefore, it is unlikely that adding perches to landslides will rapidly increase forest regeneration if no other means of facilitating growth of forest seeds such as removing grasses and climbing ferns are implemented. Longer studies are needed in order to determine if perches can be used to increase forest seedlings and to accelerate plant succession and forest recovery. Perches may be used to accelerate the accumulation of a forest seed bank on landslides in Puerto Rico, and should be erected during peak fruiting of forest species (wet season for this forest) to get the greatest positive effect.

Table 1.1. Site characteristics for the six landslides used for perch additions in the Luquillo Experimental Forest in northeastern Puerto Rico. The area for each site was determined from a rectangle using the widest dimensions. Light ( $\mu$  Einsteins  $\text{m}^{-2} \text{s}^{-1}$ ) was determined by averaging three measurements taken between noon and 2 pm local time on a clear day (<10% cloud cover) at two different heights: 1 m above the ground (which was above ground cover, if present), and at ground level.

Site	Dominant Vegetation	Elevation (m a.s.l)	Area ( $\text{m}^2$ )	Aspect	Slope ( $^\circ$ )	Light above canopy	Light at ground level
RB12	None; Bare Soil	650	506	E	34	2000	2000
MY7	None; Bare Soil	630	1120	NE	25	2700	1370
ES9	Climbing Fern	470	1444	NW	20	2300	20
ES17	Climbing Fern	440	851	NW	23	1975	60
ES15	Grass	480	1722	NW	30	2300	300
ES16	Grass	480	1295	N	18	2200	175



Table 1.2. Species of seeds collected, in perches and control plots combined, on all six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico. Seeds were classified as either bird-dispersed or wind-dispersed. Landslides where seeds were found are denoted by an X. Dominant landslide cover includes: Bare (RB12, MY7); Climbing fern (ES9, ES17); Grass (ES15, ES16).

<b>Bird-dispersed Seeds</b>	<b>Family</b>	<b>Life-form</b>	<b>RB12</b>	<b>MY7</b>	<b>ES9</b>	<b>ES17</b>	<b>ES15</b>	<b>ES16</b>	<b>% of Bird-dispersed Seeds</b>
<i>Alchornea latifolia</i>	Euphorbiaceae	Tree		X				X	5.4
<i>Clusia clusioides</i>	Clusiaceae	Tree			X	X			1.3
<i>Clusia rosea</i>	Clusiaceae	Tree		X	X			X	9.4
<i>Guarea guidonia</i>	Meliaceae	Tree			X		X	X	5.4
<i>Matayba domingensis</i>	Sapindaceae	Tree				X	X	X	6.3
<i>Miconia racemosa</i>	Melastomaceae	Shrub	X	X	X	X		X	6.8
<i>Myrsine coriacea</i>	Myrsinaceae	Tree			X			X	3.1
<i>Nectandra turbacensis</i>	Lauraceae	Tree					X	X	2.3
<i>Palicourea</i> spp.	Rubiaceae	Shrub					X	X	3.1
<i>Passiflora sexflora</i>	Passifloraceae	Vine				X			2.7
<i>Phytolacca rivinoides</i>	Phytolaccaceae	Herb		X					0.5
<i>Psychotria berteriana</i>	Rubiaceae	Shrub		X	X		X		5.9
<i>Rourea surinamensis</i>	Connaraceae	Tree					X		0.5
<i>Roystonea borinquena</i>	Araecaceae	Palm						X	1.3
<i>Schefflera morototoni</i>	Araliaceae	Tree	X			X	X	X	40.1
<i>Schlegelia brachyantha</i>	Scrophulariaceae	Vine						X	5.9
<b>Wind-dispersed Seeds</b>	<b>Family</b>	<b>Life-form</b>	<b>RB12</b>	<b>MY7</b>	<b>ES9</b>	<b>ES17</b>	<b>ES15</b>	<b>ES16</b>	<b>% of Wind-dispersed Seeds</b>
<i>Andropogon bicornis</i>	Poaceae	Graminoid	X	X	X	X	X	X	27.7
<i>Guzmania</i> spp.	Bromeliaceae	Bromeliad			X	X			<0.1
<i>Desmodium</i> spp.	Fabaceae	Herb	X	X		X	X		0.9
<i>Elephantopus mollis</i>	Asteraceae	Herb	X	X			X		0.9
<i>Homalium racemosum</i>	Flacourtiaceae	Tree						X	<0.1
<i>Lasiacis divaricata</i>	Poaceae	Graminoid				X	X	X	0.3
<i>Mikania</i> spp.	Asteraceae	Vine			X	X	X	X	0.7
<i>Paspalum conjugatum</i>	Poaceae	Graminoid	X	X	X		X	X	57.6
<i>Paspalum millegrana</i>	Poaceae	Graminoid	X	X		X	X	X	0.7
<i>Rhynchospora holoschoenoides</i>	Cyperaceae	Graminoid	X	X			X	X	10.8
<i>Tabebuia heterophylla</i>	Bignoniaceae	Tree	X	X	X	X	X	X	0.4
<i>Urena lobata</i>	Malvaceae	Herb					X		<0.1

Table 1.3. Bird-dispersed and wind-dispersed seeds per m<sup>2</sup> in perch and control plots on six landslides in the LEF, Puerto Rico (mean±SE; n=2 for each landslide site). Means were based on 14 mo seed totals.

Site	Landslide Cover	Bird-dispersed Seeds		Wind-dispersed Seeds	
		Perch	Control	Perch	Control
RB12	Bare	1.3±1.3	0	10297.7±1019.3	7648.2±5127.6
MY7	Bare	23.3±12.9	1.3±1.3	39.9±3.9	529.6±253.9
ES9	Climbing fern	19.3±14.2	0	37.4±14.2	50.3±6.4
ES17	Climbing fern	20.6±7.7	1.3±1.3	56.7±12.9	97.9±67.0
ES15	Grass	110.8±38.7	0	2819.6±667.5	1970.4±14.2
ES16	Grass	117.3±64.4	0	1662.4±1164.9	2757.7±1113.4

Table 1.4. Bird species observed in the six landslides used for perch additions. The \* symbol indicates birds that were observed on the perches and the respective landslide where the observation(s) took place, and X indicates landslides where each bird was observed.

Species	Family	RB12 (bare)	MY7 (bare)	ES9 (fern)	ES17 (fern)	ES15 (grass)	ES16 (grass)
Bananaquit ( <i>Coereba flaveola</i> )	Emberizidae	X	X	X	X*	X	X
Black-cowled Oriole ( <i>Icterus dominicensis</i> )	Emberizidae						X
Black-faced Grassquit ( <i>Tiaris bicolor</i> )	Emberizidae	X*	X	X	X*	X*	X*
Black-whiskered Vireo ( <i>Vireo altiloquus</i> )	Vireonidae					X	
Caribbean Martin ( <i>Progne dominicensis</i> )	Hirundinidae						X
Gray Kingbird ( <i>Tyrannus dominicensis</i> )	Tyrannidae		X		X	X*	X*
Green Mango ( <i>Anthracothorax viridis</i> )	Trochilidae	X	X	X	X	X	
Pearly-eyed Thrasher ( <i>Margarops fuscatus</i> )	Mimidae	X	X	X		X	X
Pigeon/Dove (Columbidae)	Columbidae	X	X	X	X	X	
Puerto Rican Bullfinch ( <i>Loxigilla portoricensis</i> )	Emberizidae			X	X	X	
Puerto Rican Emerald ( <i>Chlorostilbon maugaeus</i> )	Trochilidae	X*	X	X	X*	X	X
Puerto Rican Flycatcher ( <i>Myiarchus antillarum</i> )	Tyrannidae				X		
Puerto Rican Lizard-Cuckoo ( <i>Saurothera vieilloti</i> )	Cuculidae		X				
Puerto Rican Tanager ( <i>Nesospingus speculariferus</i> )	Emberizidae	X	X	X*	X	X	X
Puerto Rican Toady ( <i>Todus mexicanus</i> )	Todidae			X			X
Puerto Rican Woodpecker ( <i>Melanerpes portoricensis</i> )	Picidae		X	X	X	X	
Red-legged Thrush ( <i>Turdus plumbeus</i> )	Muscicapidae				X		
Red-tailed Hawk ( <i>Buteo jamaicensis</i> )	Accipitridae				X	X	X
Scaly-naped Pigeon ( <i>Columba squamosa</i> )	Columbidae	X	X	X	X	X	X
Shiny Cowbird ( <i>Molothrus bonariensis</i> )	Emberizidae						X
Stripe-headed Tanager ( <i>Spindalis zena</i> )	Emberizidae	X	X*			X	
White-winged dove ( <i>Zenaida asiatica</i> )	Columbidae					X	
Yellow-faced Grassquit ( <i>Tiaris olivacea</i> )	Emberizidae						X*

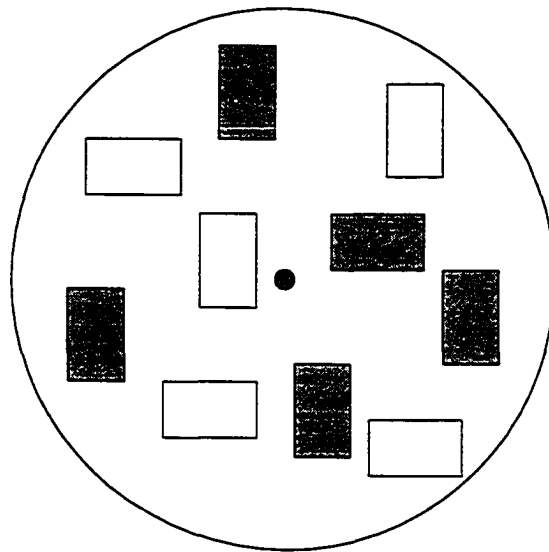
Table 1.5. Bird visitation frequency to perches per hour of observation at six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico (mean  $\pm$  SE). Visitation frequencies were based on five total hours (morning and afternoon) of bird observation per landslide.

Landslide	Vegetation Cover	Perch Visitation Hour <sup>-1</sup>
RB12	Bare	0.83 $\pm$ 0.40
MY7	Bare	0.17 $\pm$ 0.40
ES9	Climbing fern	1.33 $\pm$ 0.84
ES17	Climbing fern	1.67 $\pm$ 0.67
ES15	Grass	1.33 $\pm$ 0.49
ES16	Grass	2.17 $\pm$ 0.79

Table 1.6. Profile contrasts ( $time_2 - time_1$ ) of percent ground cover of five cover characteristics sampled at two time periods on six landslides in the LEF, Puerto Rico. A significant P-value for the mean of the contrast indicates temporal change in cover averaged across landslide types (grass, climbing fern, bare). A significant P-value for landslide type represents variation among landslide types in temporal change of ground cover. All main effects and interactions in the MANOVA were significant ( $P < 0.0001$ ).

Source	df	Bare	Ferns	Graminoids	Shrubs+Herbs	Litter
Mean	1	<0.0001	<0.0001	0.0027	<0.0001	<0.0001
Landslide Type	2	<0.0001	0.0045	0.3500	0.0246	0.5416

Figure 1.1. Schematic of perch or non-perch control plot with seed baskets (shaded boxes) and short-term succession subplots (unshaded boxes). The circular plot (2 m diameter) was centered around the perch stem for perch plots or the center of control plots.



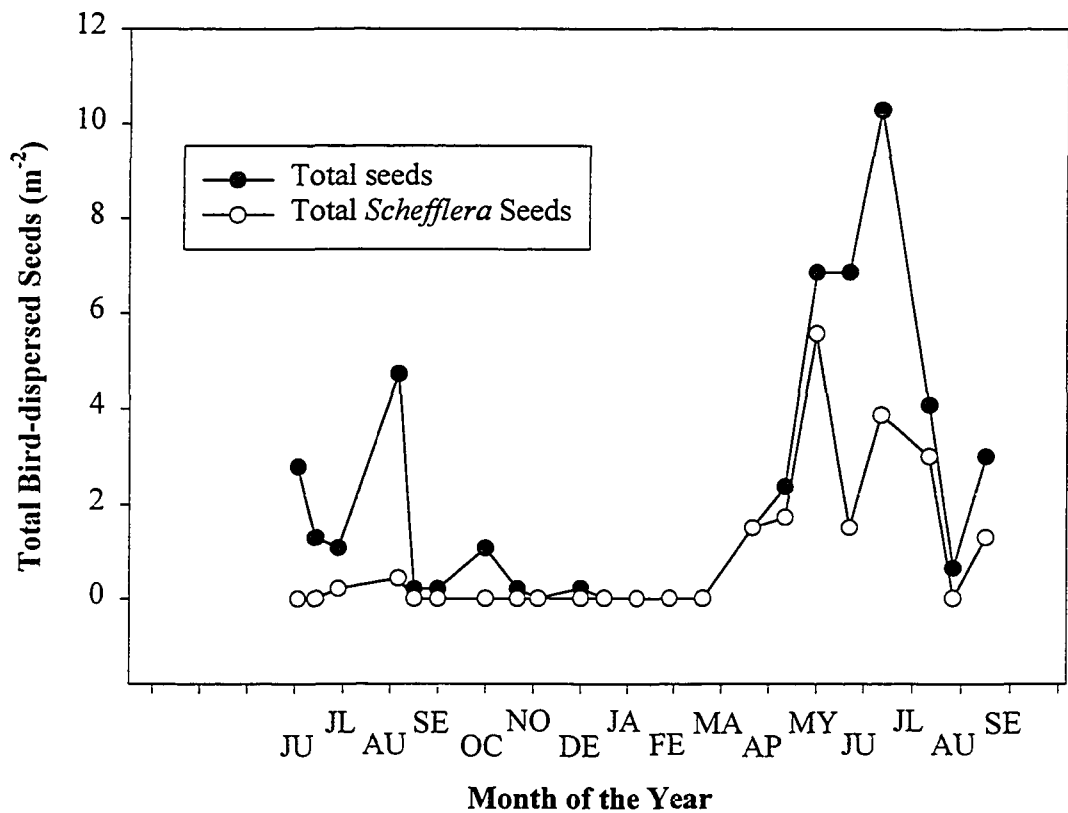


Figure 1.2. Total bird-dispersed seeds (including *Schefflera*) per m<sup>2</sup> and total *Schefflera* seeds per m<sup>2</sup> retrieved at bird perch plots for each collection period on six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico. Seeds were collected approximately every three weeks beginning 14 June 2000 and ending 17 June 2001.

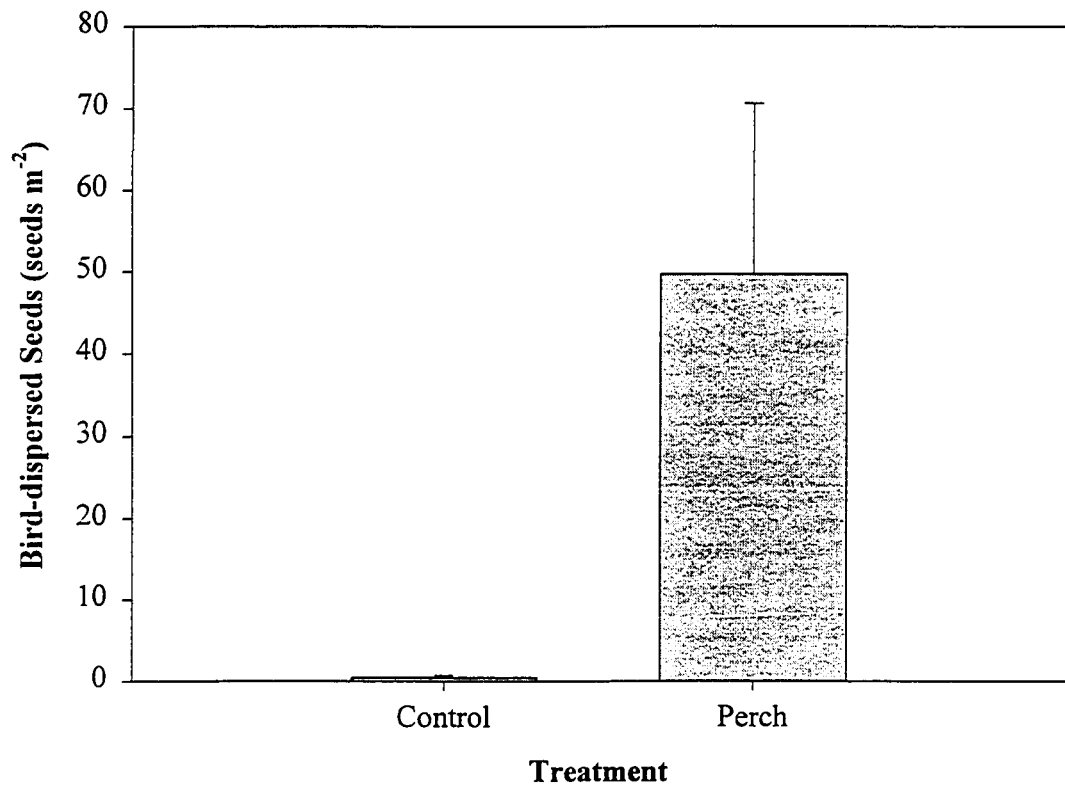


Figure 1.3. Bird-dispersed seeds per m<sup>2</sup> for perch and control plots in six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico (mean  $\pm$  SE; n = 6). The difference between the treatment means is significant ( $P = 0.005$ ).



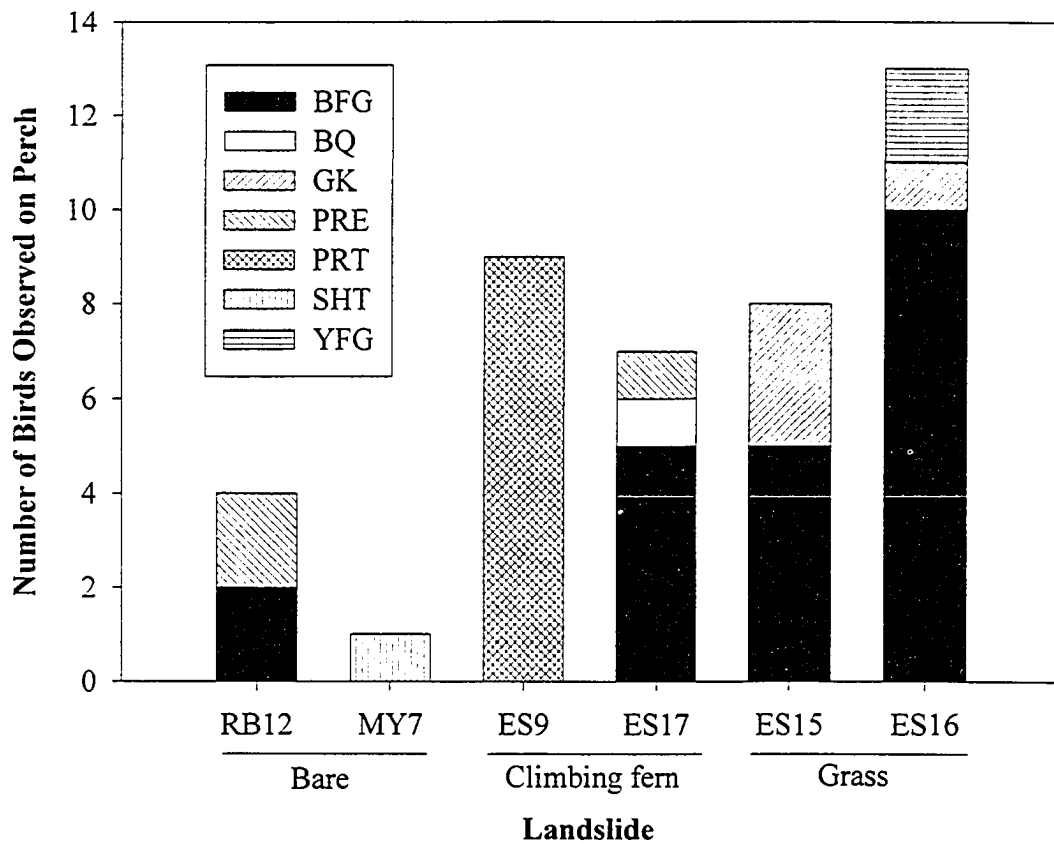


Figure 1.4. Total number of birds observed on perches during 5 hours of observation at each of the six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico. Bird species include: BFG = Black-faced Grassquit; BQ = Bananaquit; GK = Gray Kingbird; PRE = Puerto Rican Emerald; PRT = Puerto Rican Tanager; SHT = Stripe-headed Tanager; YFG = Yellow-faced Grassquit.

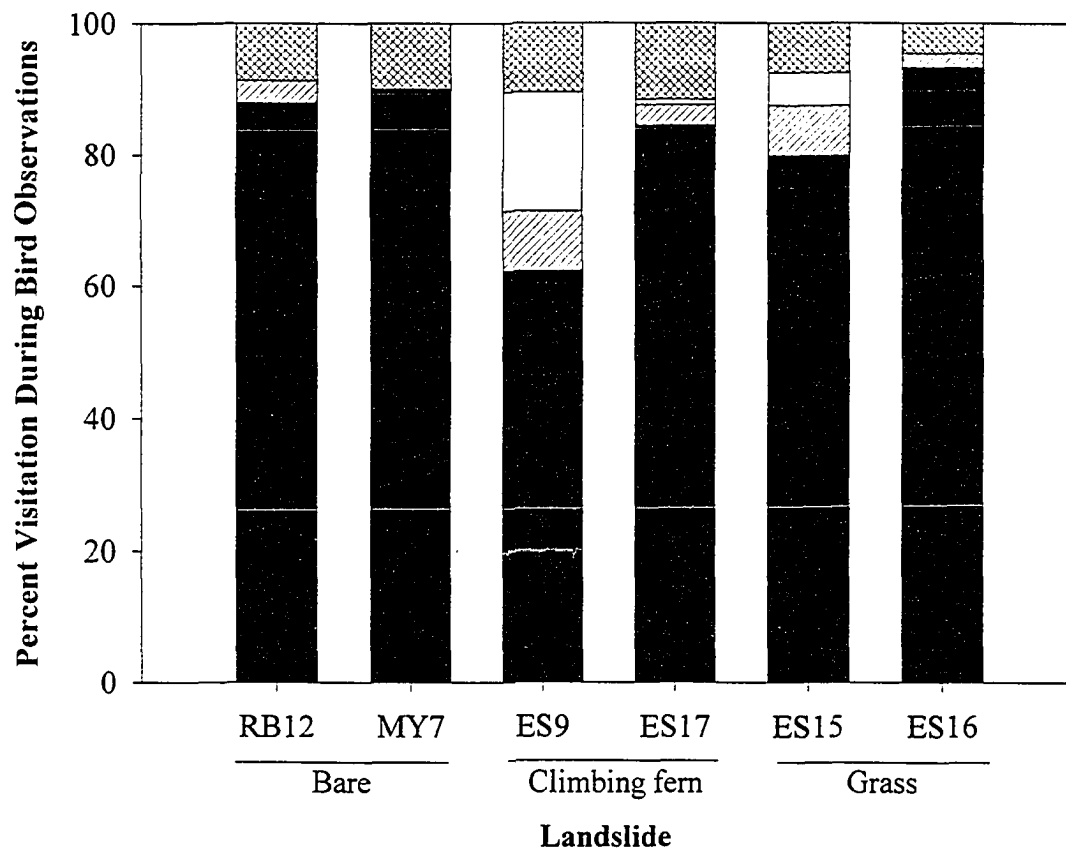


Figure 1.5. Mean percent visitation of birds observed at each of four locations (solid = forest edge; diagonal = artificial perch; white = natural perch on landslide; cross-hatch = flying) in six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico.

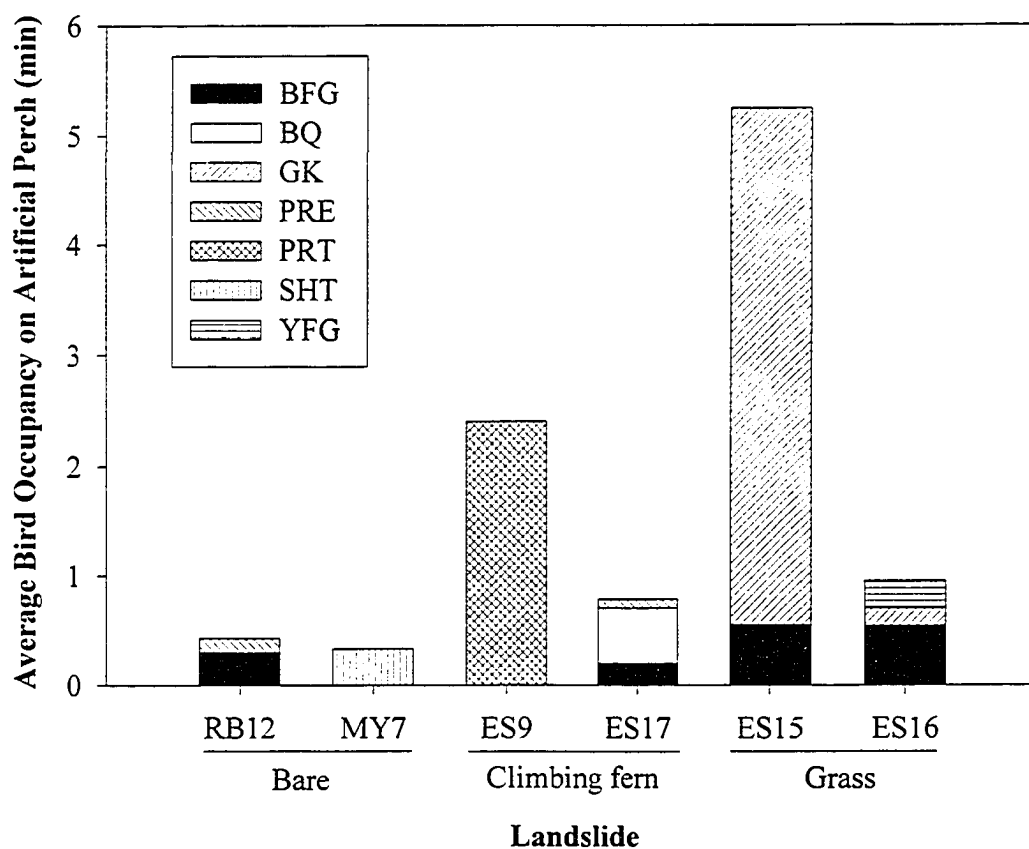


Figure 1.6. Average visitation time (minutes) of birds on perches in the six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico. For each landslide, 5 hours (300 minutes) of total observation took place. See Fig. 1.4 for the number of individuals represented. BFG = Black-faced Grassquit; BQ = Bananaquit; GK = Gray Kingbird; PRE = Puerto Rican Emerald; PRT = Puerto Rican Tanager; SHT = Stripe-headed Tanager; YFG = Yellow-faced Grassquit.

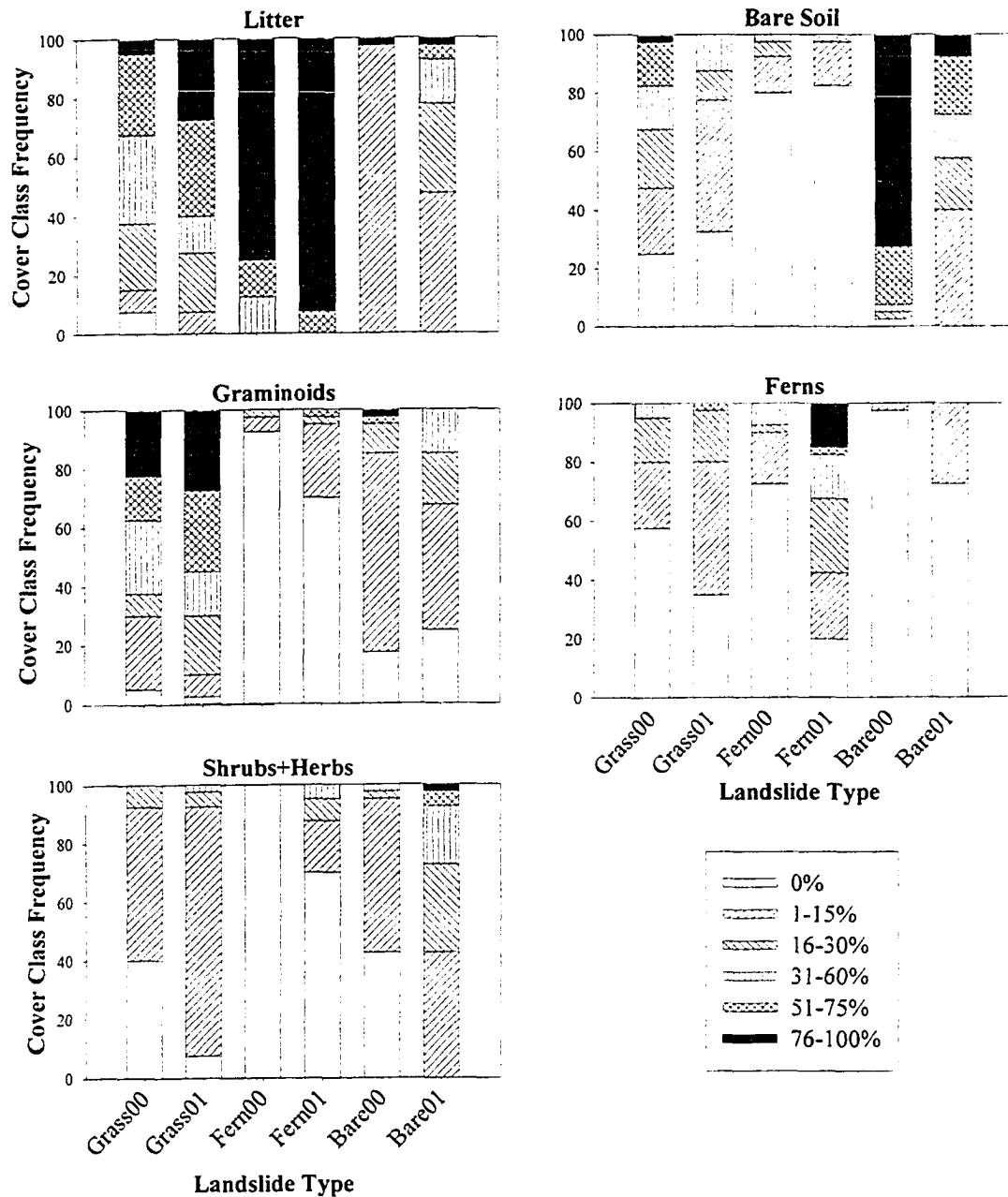


Figure 1.7. Cover class frequency of litter, bare soil, graminoids, ferns, and herbs on three different landslide types during two time periods (July 2000: 00, August 2001: 01). Cover class frequencies were determined from measurements of 40 subplots for each landslide type.

## CHAPTER 2

# RESPONSES OF SEEDS, SEEDLINGS, AND SOILS TO ORGANIC MATTER AND FERTILIZER ADDITIONS IN LANDSLIDES

### Introduction

Landslides, one of the most severe natural disturbances in tropical rainforests (Garwood et al., 1979; Walker et al., 1996; Myster & Walker, 1997; Restrepo & Vitousek, 2001), are common in montane regions of the Caribbean and are usually triggered by high rainfall events, such as those that accompany hurricanes and tropical storms (Larsen & Simon, 1993; Larsen & Torres-Sánchez, 1996; Walker et al., 1996). Landslides generally result in the loss of at least the litter and topsoil layer of the soil profile (O- and A-horizons) as well as most existing vegetation. This causes increased surface runoff (Larsen & Torres-Sánchez, 1990), high susceptibility to further erosion (Larsen & Torres-Sánchez, 1996; Walker et al., 1996), and nutrient loss (Guariguata, 1990; Walker et al. 1996).

Organic matter is one of the primary sources of nutrients in tropical rainforests (Vitousek & Sanford, 1986) and landslides remove the topsoil, organic matter, and

associated nutrients, resulting in soils of lower nutrient levels than those soils in adjacent undisturbed forest (Adams & Sidle, 1987; Guariguata, 1990; Dalling & Tanner, 1995; Walker et al., 1996). Additionally, sources of organic matter inputs to recent landslides are minimal, and include: litterfall from surrounding vegetation in the nearby forest. litterfall from existing landslide vegetation, patches or islands of remaining organic matter that were not completely removed by the disturbance, and forest soil transported onto the landslide by erosional processes. The rate of organic matter accumulation affects soil development, and older landslides have greater soil development than younger landslides (Zarin & Johnson, 1995). With increased soil development, nutrients that are essential for plant growth also increase (Sanchez, 1976; Kielland, 1994; Tiessen et al., 1994; Chapin, 1995; Vitousek & Farrington, 1997; Berendse et al., 1998). Because soil nutrients directly affect plant growth, it has been hypothesized that organic matter, as a nutrient source, is one of the most limiting factors in plant colonization on landslides in Puerto Rico (Walker et al., 1996).

Despite the importance of organic matter as a nutrient source to landslides, soil nutrients other than commercial fertilizer have not been added to landslides in the Caribbean. However, mulches have been experimentally added in many situations in temperate ecosystems to increase seedling growth and survival (e.g., coastal scrub, Zink & Allen, 1998; grassland, Windsor & Clements, 2001), and municipal wastes have been added as an organic matter treatment to successfully stimulate seed germination and plant growth (Roberts & Roberts, 1986; Marchiol et al., 1999). In this study, I tested the effects of organic mulch (leaf litter), mature forest soil, and commercial fertilizer on landslide soil fertility, seed germination, and seedling growth.

Decomposition of plant material may take months or years (Vogt et al., 1986; Bloomfield et al., 1993; Silver & Vogt, 1993) and the degree of decay and quality of the organic matter directly influences the release of nutrients (Nziguheba et al., 1998). During decomposition, nutrients bound in organic matter may either become available for plant uptake through mineralization (Sanchez, 1976; Tiessen et al., 1994), or unavailable to plants through leaching (Silver et al., 1996), adsorption (Sollins et al., 1988), or immobilization (Vitousek & Matson, 1984; Zimmerman et al., 1995; Zink & Allen, 1998; Reeve Morghan & Seastedt, 1999). Particularly in areas that lack vegetation and experience wet climates, nutrient concentrations in soil and soil solution are commonly lost through leaching (Uhl & Jordan, 1984; Silver et al., 1996). Adsorption occurs when nutrients are geochemically fixed, which is particularly common for P in tropical soils (Uehara & Gillman, 1981; Sollins et al., 1988). Microbial immobilization occurs when nutrients are utilized by soil microorganisms, and are therefore unavailable for plant uptake (Binkley & Vitousek, 1989).

In general, soils nutrients, especially nitrogen (N) and (P), are often at low levels in tropical ecosystems (Vitousek, 1984; Vitousek & Sanford, 1986; Herbert & Fownes, 1995; Lewis & Tanner, 2000). Fetcher et al. (1996) determined N and P limits plant growth on a Puerto Rican landslide. Guariguata (1990) found landslides had low levels of total soil N and plant available P, correlating with low soil organic carbon, when compared to soils from the forest understory in Puerto Rico. On a chronosequence of landslides in Puerto Rico, plant available P increased with landslide age and landslide age was correlated with increased carbon (Frizano et al., 2002).

Nutrients are occasionally necessary for seed germination. Nitrate ( $\text{NO}_3^-$ ) is the most common soil chemical that promotes seed germination (Schimpf & Palmbald, 1980; Fenner, 1985; Hilhorst & Karssen, 2000). In tropical ecosystems, increased  $\text{NO}_3^-$  concentrations increased germination of some species (Uhl & Clark, 1983; Orozco Segovia, 1986). Of 85 weed species tested by Steinbauer and Grigsby (1957), half showed increased germination due to  $\text{NO}_3^-$ . However, in many cases it is  $\text{NO}_3^-$  with the combination of other germination cues, such as light and moisture, that stimulates seed germination (Fenner, 1985).

Seedling growth in tropical forests is generally limited by light (Augsburger, 1984; Popma & Bongers, 1988; Uhl et al., 1988). Growth of seedlings in disturbed areas with high light, such as treefall gaps and landslides (Chazdon & Fetcher, 1984; Fernández & Myster, 1995), is more likely to be responsive to nutrient additions than growth of seedlings in lower light conditions of the forest understory (Chapin, 1980; Denslow et al., 1990; Turner et al., 1993; Dalling & Tanner, 1995). Fertilizer additions to landslides have facilitated seedling growth in Jamaica (Dalling & Tanner, 1995) and in Puerto Rico (Fetcher et al., 1996). However, growth rates of seedlings in treefall gaps in Costa Rica did not respond to fertilizer, perhaps due to light limitations (Denslow et al., 1990).

If soil nutrients are limiting to plant growth in Caribbean landslides, as proposed by Walker et al. (1996) and demonstrated previously by Dalling and Tanner (1995) and Fetcher et al., (1996), fertilizer additions and organic matter, such as mulch and forest soil could increase plant establishment and growth as well as potentially accelerate landslide revegetation. This study specifically addressed the following two hypotheses:

- 1) Soil fertility (especially N and P) of Puerto Rican landslides is altered by additions of



organic matter and soil nutrients. 2) Plant colonization and plant growth in landslides is limited by nutrient availability. The first hypothesis was tested by adding commercial fertilizer and three types of organic matter that represent “natural” inputs to landslides in Puerto Rico (i.e., forest soil and two types of leaf litter), followed by repeated soil sampling to determine soil fertility. I predict that all treatments will increase soil fertility in the following order: commercial fertilizer>forest soil>leaf litter>control. To test the second hypothesis, the same treatments were mixed in landslide soils and then seeded. I predict the order of plant height and growth will be as follows: commercial fertilizer>forest soil>leaf litter>control. Lastly, based on the readily available  $\text{NO}_3^-$  and the results of Fetcher et al. (1996) where fertilizer accelerated the landslide soil seed bank, commercial fertilizer is predicted to increase seed germination compared to the remaining treatments.

## Materials and Methods

### Study Site

This study was conducted on five landslides in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico ( $18^\circ 15' - 18^\circ 23' \text{N}$ ,  $65^\circ 52' - 65^\circ 48' \text{W}$ ) where mean annual precipitation is 3000-4000 mm with high year-to-year variation and little seasonality. Mean monthly temperatures range from 21-25°C (Brown et al., 1983; Soil Survey Staff, 1995). The landslides used in this study were between 460-750 m a.s.l. Below 600 m elevation the vegetation is subtropical wet forest (Ewel & Whitmore, 1973), characterized by tabonuco (*Dacryodes excelsa*), ausubo (*Manilkara bidentata*), and motillo (*Sloanea berteriana*) trees. Above the average cloud condensation level of

600 m, the vegetation is subtropical rain forest, characterized by palo colorado (*Cyrilla racemiflora*) and patches of palm (*Prestoea montana*) (Waide & Lugo, 1992). Botanical nomenclature follows Liogier and Martorell (1982) and Taylor (1994).

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*, *Shefflera*, and *Miconia*. A more detailed description of landslide vegetation in the LEF is found in Walker (1994) and Walker et al. (1996).

A landslide is defined as the displacement of a mass of ground that creates a defined surface of rupture (Varnes, 1978). Although aerial photographs can be used to estimate ages of landslides in the LEF (Guariguata, 1990), dating landslides has generally proved difficult due to secondary erosion and re-sliding (Walker et al., 1996). Therefore, ages of landslides in this study were not specified, but were estimated to be <5 yr old based on the proportion of bare ground cover within the landslide area. I chose five landslides at random among all landslides in the LEF that had <30° slopes, had an area of bare soil (<20% plant cover) at least 14 m<sup>2</sup>, and that were accessible (<500 m from a road or trail). Landslides varied in parent material, soil type, dominant vegetation, and physical and microclimate properties (Table 2.1). One landslide was located in the Río Blanco drainage (RB10), one in the Río Mameyes (MY8), two in the Río Espíritu Santo drainage (ES5, ES10), and one in the Río Jiménez drainage (J4). Two landslides (RB10 and MY8) had Inceptisols derived from quartz-diorite bedrock, and the other three landslides (ES5, ES10, J4) had Ultisols derived from volcanoclastic bedrock (Seiders, 1971). Both soil

types have been documented as acidic, silty clay loams that remain continuously wet, have low permeability, and high susceptibility to slippage (Boccheciamp, 1977).

### Soil Amendments

Four soil amendments were applied to each of the five landslides in a field experiment and a parallel screen-house experiment (see below) in order to measure the effects on seeds, seedlings, soil nutrients, and plant succession. The four amendments were: additions of dried leaves of either *Cecropia schreberiana* (Moraceae), additions of dried fronds of *Cyathea arborea* (Cyatheaceae), additions of forest soil, and additions of commercial fertilizer. Treatments were mixed with landslide soil to 10 cm depth, then placed in bottomless aluminum trays buried to 6 cm depth to permit leaching, and *ca* 0.5 cm of the tray edge remained above the ground surface to retard overland flow leading to potential treatment loss on the five landslides. Aluminum trays were of two sizes: small (10 x 20 cm) and large (20 x 20 cm). Small trays were used for measuring seed and seedling responses to treatments, and large trays were used to obtain enough soil for year-long soil sampling used to determine soil chemical and physical responses to treatments. Treatment quantities were determined by adding three times the total nitrogen (N) found in annual non-hurricane litterfall in the El Verde portion on the LEF (Lodge et al., 1991), which amounted to 0.39 g N (25.92 g litter year<sup>-1</sup>) to a 10 x 20 cm area (small tray size). Therefore, for each soil treatment used (*Cecropia*, *Cyathea*, forest soil, commercial fertilizer), the N concentration was determined from previous studies in the LEF such that 0.39 g N was added to each small tray. Large trays had two times the amount of each treatment added (0.78 g N). For the control soil treatments, existing soil was only mixed to 10 cm depth and replaced *in situ* within the bottomless tray.

*Cecropia*, a dominant pioneer tree in forest gaps and landslides, and *Cyathea*, a common tree fern on landslides, both contribute to forest succession with their rapid growth and recycling of soil nutrients (Lawrence, 1996; Brokaw, 1998; L. Walker, *unpublished data*). Recently senesced leaves (i.e., leaf litter) were collected from LEF roadsides in May 2000 from at least 20 different plants per species, dried at 40°C for 7 d, then cut into <math><1\text{ cm}^2</math> pieces. *Cecropia* (1.5% N; Scatena et al., 1993) leaf blade and petiole, and *Cyathea* (1.2% N; L. Walker, *unpublished data*) pinnae and rachis, were added in proportions that mimicked their natural leaf parts (i.e., blade and petiole for *Cecropia*; pinnae and rachis for *Cyathea*) on a dry-weight basis. Therefore, for each small aluminum tray, the following treatments (dry weights) were added: 26 g *Cyathea* (17.3 g rachis, 8.7 g frond), and 26 g of *Cecropia* (5.6 g petiole, 20.4 g blade).

Forest soil was added to test its importance as an input to landslides. Forest soil enters landslides from the surrounding edges and sometimes remains in patches following landslide slippage. I collected soil from six randomly chosen 40 x 40 x 5 cm deep plots in a mature section of the LEF dominated by *Dacryodes* trees after first removing the O-horizon and any organic material >2 mm diameter. The soil was not sterilized in order to simulate natural additions of forest soil to landslides. For small treatment trays, 78 g of forest soil (0.5% N dry weight; Heyne, 2000; 123 g field moist) was added.

Commercial fertilizer (hereafter referred to as fertilizer) was added to test its effect as a readily accessible nutrient source that could be used in future restoration of landslides. To each small tray I added 2.16 g of Dynamite Plant Food™, a polymer-resin coated, 6-month, time-release fertilizer. The nutrient content of the fertilizer was as follows: total nitrogen 18% (8.6% as  $\text{NH}_4$ , 9.4% as  $\text{NO}_3$ ), available phosphorus (as  $\text{P}_2\text{O}$ ) 6%, soluble

potash (as  $K_2O$ ) 8%, magnesium 1.2%, boron 0.02%, copper 0.05%, iron 0.20%, manganese 0.06%, and molybdenum 0.02%.

Following treatment additions to landslides, I conducted total N analysis on the *Cecropia* and *Cyathea* leaves, and forest soil samples used in the soil treatment experiment in order to obtain more accurate N contents of these treatments. Samples were ground and passed through a 1 mm mesh sieve, digested using the Kjeldahl digestion procedure, and analyzed colorimetrically using an Alpkem Analyzer (Alpkem Corporation, 1992). Foliar pH content of *Cecropia* and *Cyathea* was measured by mixing 1 g of ground vegetation with 5 mL of deionized water to form a 1:5 paste. The 1:5 ratio was necessary to saturate the foliar material so that it could be analyzed using the glass probe of the pH meter.

#### Experimental Design

Areas of at least 3 x 6 m were cleared of any existing vegetation on the upper, mostly bare portions of the chosen landslides. Treatments were assigned within trays on a landslide at random, and each tray was 10 cm from adjacent trays and 20 cm from trays above or below it (Fig. 2.1). In total, 225 small trays were arranged over the five sites (five landslides x five soil treatments x three seed treatments x three replicates) and 75 large trays were arranged over the sites (five landslides x five soil treatments x three replicates). All treatments were added to the five landslides between 11-16 June 2000.

In order to test the effect of organic matter and fertilizer treatments under more controlled conditions, a screen-house experiment was set up at El Verde Field Station (EVFS; 350 m a.s.l.). Two 1.2 x 3.2 m benches were positioned in the area of highest light exposure (i.e., middle of forest gap) in an abandoned coffee terrace adjacent to

EVFS in an effort to mimic high-light conditions that are characteristic of recent landslides (Table 2.1). Fiberglass mesh screening (1mm x 2mm mesh) was used to cover the side-walls and top of the bench to keep out litterfall and seeds of most sizes, while creating minimal shading ( $1110 \mu \text{ Einsteins m}^{-2} \text{ s}^{-1}$  inside vs.  $1800 \mu \text{ Einsteins m}^{-2} \text{ s}^{-1}$  outside the screen-house on a cloudless day). Treatment tray locations for the screen-house experiment were also determined in a random fashion. Instead of removing the bottoms, five holes (*ca* 0.7 cm diameter) were punched in the bottoms of each small aluminum tray used in the screen-house experiment to permit leaching.

Soil treatment concentrations added to small trays in the screen-house experiment were identical to those added in the field experiment. Soil used to fill each tray to 5 cm depth in the screen-house experiment was obtained from a recent (<6 mo) landslide along a road in the LEF, close to landslides ES5 and ES10. Treatments were added on 25 July 2000. In total, 120 small trays were used in the screen-house experiment (five soil treatments x three seed treatments x eight replicates). Only small aluminum trays (10 x 20 cm) were used, as only one soil sampling took place in the control seed treatment trays (i.e., no seeds added) following one year after original soil treatment addition.

#### Field Soils

Landslide soils in the field experiment were sampled within the large aluminum trays to the same 10 cm depth of the original treatment using a 1.9 cm diameter corer. Soils were sampled just prior to soil treatment addition, then 60, 210, and 370 d following treatment additions for soil organic matter (SOM), total N, available P, total P, pH, moisture. Soils were also sampled at 45 d and 360 d for ammonium ( $\text{NH}_4^+$ ), nitrate

( $\text{NO}_3^-$ ), and the rate of N-mineralization (described below). For each sampling period, two cores were taken from each aluminum tray and pooled. The location of soils sampled within each tray was randomized except that to account for leaching due to landslide slope, one soil core was taken on the upslope side of each tray, and the second core was taken on the downslope side of each tray. Neither surrounding soil nor debris was replaced in cored holes upon sampling to minimize nutrient alterations. All soil samples for a given sampling period were taken on the same day; however, soil sampling only occurred if there was not significant rainfall in the LEF during the previous 24 h. Periodic removal of any vegetation (i.e., weeding) occurred throughout the experiment to minimize the loss of soil nutrients due to plant growth.

To determine plant available nitrogen (i.e.,  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) and the rate of N-mineralization, *in situ* incubations were made for each tray. Sampling took place 45 and 360 d following treatment additions. Methods for assessing N-mineralization provide an index of the amount of inorganic N converted from organic matter in a given environment over a specific time period (Binkley & Vitousek, 1989). Two cores of soil to 10 cm depth were taken simultaneously from each tray no more than 3 cm apart. One soil core (pre-incubation sample) was taken back to EVFS (kept cool in a cooler) and immediately extracted with 2M KCl following methods in Binkley and Vitousek (1989). The second sample (post-incubation sample) was double-bagged using polyethylene bags, replaced into the soil and incubated *in situ* for 14 d, then collected and extracted in the same manner as the pre-incubation sample. The polyethylene bags used for the field incubation allowed gas transfer while preventing water and nutrient gain or loss during the 14 d period. Thus, field temperatures are reflected in the bags, and moisture content

is held constant throughout the incubation (Binkley & Vitousek, 1989). *In situ* incubations were favored over laboratory incubations due to variable landslide characteristics (Table 2.1) that likely influence the soil microclimate properties between sites. However, a laboratory incubation experiment at EVFS was also conducted in order to measure N-mineralization in more controlled conditions by collecting samples from all sites on 7 August 2001, followed by a 10 d laboratory incubation. The laboratory aerobic incubation followed the methods of Kandeler (1996) where 1-2 mL of deionized water was added dropwise (avoiding puddling) to 10 g of field moist soil in 200 mL flasks. Flasks were then loosely capped to allow gas exchange, and stored at  $24 \pm 1.5^\circ \text{C}$ . An additional 1-2 mL of deionized water (depending on visual soil condition) was added after 5 d of incubation to prevent soils from drying out. Post-incubation 2 M KCl extraction was conducted in the same manner as described above.

Gravimetric soil moisture was determined immediately following sampling (Topp, 1993). Soil particle size (Sheldrick & Wang, 1993) was measured on soils to 10 cm depth ( $n=3$  for each landslide) from unaltered areas on 10 August 2001. The one modification from this method was that the clay reading was taken after 2 h of settling time instead of 7 h. Soil bulk density ( $\text{g cm}^{-3}$ ) was determined using soils (10 cm depth;  $25.6 \text{ cm}^{-3}$ ) from landslide treatment trays 370 d following soil treatments.

Two different methods were used to determine SOM. The loss-on-ignition (LOI) method (Nelson & Sommers, 1996) was used following the procedure outlined in Karam (1993) for all soils sampled during each sampling period. One problem with the LOI method is that SOM is often overestimated with soils of high clay content (Howard & Howard, 1990; Karam, 1993; Nelson & Sommers, 1996) as a result of tightly held water



molecules in clays being burned off at temperatures exceeding 300-350° C (Ranney, 1969; Gallardo et al., 1987). Moreover, these soils were from the upper portion of recently eroded landslides where organic matter is minimal (Guariguata, 1990), and results from the LOI method for these soil showed high SOM values that also correlated with high clay content. Because of this possible error, I also used a second method, the hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) digestion method (USDA, 1996; Sheldrick & Wang, 1993), on a subset of soils to determine a more accurate estimate of SOM. Samples used for the H<sub>2</sub>O<sub>2</sub> method were the same used in the LOI from the 60 d sampling period. The limitation with this method is that it often underestimates SOM by not completely oxidizing organic matter (Nelson & Sommers, 1996). Furthermore, the LOI method is rated a more robust method overall compared to the H<sub>2</sub>O<sub>2</sub> method (Nelson & Sommers, 1996), and therefore was used to compare treatment differences for each sampling period.

Estimation of available soil phosphorus (PO<sub>4</sub><sup>3-</sup>) followed the Bray-1 test (Bray & Kurtz, 1945). This method is appropriate for these soils because they are acidic and likely have significant amounts of phosphorus (P) bound to iron and aluminum. The NH<sub>4</sub>F dissolves aluminum and iron phosphates in acid solution (Olsen & Sommers, 1982; Kuo, 1996). Available soil P was extracted from these soils by the method described in Kuo (1996); I shook 4 g of soil (previously heated for 24 h at 40° C) for 60 s in 25 mL of extracting solution containing 0.03 M NH<sub>4</sub>F and 0.025 M HCl.

In order to determine total N and total P of the soil, samples were digested in a sulfuric acid medium and analyzed colorimetrically using an Alpkem Segmented Flow Analyzer for determination of total Kjeldahl N and total Kjeldahl P (Alpkem Corporation, 1992). Levels of NH<sub>4</sub><sup>+</sup> and levels of NO<sub>3</sub><sup>-</sup> plus NO<sub>2</sub><sup>-</sup> (NO<sub>2</sub><sup>-</sup> was reduced to

NO<sub>3</sub><sup>-</sup> by cadmium reaction) were determined from KCl extractions using an Alpkem Analyzer (Alpkem Corporation, 1992). Available P was determined from the Bray-1 extraction using an Alpkem Analyzer (Alpkem Corporation, 1992).

Soil pH was determined by mixing 5 g of soil to 5 mL of deionized water to make a 1:1 paste, which was measured with a glass probe pH meter, following the methods of Hendershot and Lalande (1993) with the modification that samples were mixed for 30 seconds then allowed to stand for 2 min before measuring.

### Decomposition

A year-long decomposition experiment was set up to determine *Cecropia* and *Cyathea* leaf degradation on landslides. The foliar material used in this experiment was from the same sampling batch that was used in the field soil treatment trays and in the screen-house experiment. Litter of each species had been dried at 40°C to a constant weight, as well as cut into pieces approximately 1 cm<sup>2</sup>. Decomposition bags (litterbags) were constructed using fiberglass screening (2mm x 1mm mesh). A total of 5 g of leaf material was added to each 0.012 m<sup>2</sup> (12 cm x 10 cm) litterbag in proportions representative of their natural leaf parts (determined and described above). Therefore, *Cecropia* litterbags contained 1.07 g of petiole and 3.93 g blade, and *Cyathea* litterbags contained 3.33 g rachis and 1.67 g pinnae. 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 x 5 sampling periods x 3 replicates x 2 species) were constructed, filled, and placed on the upper portions (i.e., bare soil areas) of the same five landslides used for soil treatment additions. Two randomly chosen plots within

each landslide site were used to divide the litterbags. 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 10 cm in each direction separated adjacent litterbags. In order to account for any lost foliar mass due to handling litterbags between EVFS and the field sites, 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 but keep the foliar material inside the bags, 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 experiment. 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 littermass.

Samples of *Cecropia* and *Cyathea* littermass from the 365 d sampling were analyzed for total N and total P using the Kjeldahl digestion procedure and colorimetric analysis described above (Alpkem Corporation, 1992).

#### Screen-house Soils

For the screen-house experiment, soils were sampled one year following initial soil treatment on 13 August 2001. Soils were sampled to 5 cm depth with a trowel in trays that did not have any seed addition (n=40). Analyses of screen-house soils followed methods described in the field experiment, and the soil variables that were measured included: SOM (LOI method), total N, total P, available P, pH, moisture, and particle size.

### Field Plant Responses

Seeds of two plant species were used to test whether soil treatment additions to landslide soil affects germination and establishment and growth of seedlings. *Phytolacca rivinoides* (Phytolaccaceae) is a common herb in disturbed areas in the LEF, such as landslides and treefall gaps, that has a sprawling physiognomy generally up to *ca* 3 m wide and *ca* 1.5 m tall. *Paspalum millegrana* (Poaceae) is a perennial grass reaching heights of 1.5 m that is common to disturbed areas such as landslides and roadsides. Seeds of each species were collected in May 2000 from >5 individuals within the tabonuco forest near the EVFS (*Phytolacca*) or from >15 individuals from roadsides throughout the LEF (*Paspalum*).

The germination experiment began 15-17 June 2000 by randomly assigning small trays on each landslide one of the following seed treatments: *Phytolacca* seeds, *Paspalum* seeds, or unseeded controls. In each tray, 100 seeds (determined by mass) were pressed lightly into the soil surface. Seed germination, determined as at least the emergence of a radical, was monitored on each landslide every 4-6 d, between 27 June and 12 August 2000, and new germinants were removed. Germination was reported as percent of viable seeds sown (viability was determined in petri dishes and potting soil at the EVFS during June-August 2000).

Seeds were sown a second time on 14-15 October 2000, to measure seedling establishment (seedlings established per viable seeds sown) and growth. Based on results of the germination experiment, 30 seeds were sown in each tray in order to get approximately six established seedlings per tray. Prior to sowing, weeding of any existing seedlings was conducted for all trays. Re-seeding the trays after the germination

experiment was favored rather than re-mixing soil treatments at new landslide sites because of the intense labor involved in setting up such an experiment, as well as the lack of available landslides on which to conduct these experiments.

Eighty days after sowing (3-6 January 2001), established *Paspalum* and *Phytolacca* seedlings were thinned at random to a maximum of six individuals per tray, marked, and measured for height (cm) from the soil-shoot interface to the tallest foliar structure. After 235 d following seed sowing, percent survival of seedlings since the January 2001 thinning was calculated, as well as seedling height, and total biomass. Total biomass was determined by drying roots and shoots for 5 d at 60°C. Samples were weighed as a composite seedling biomass for a given sample tray, then divided by the number of individual seedlings to get mass individual<sup>-1</sup>.

#### Screen-house Plant Responses

For the screen-house experiment, *Paspalum*, *Phytolacca*, and control seed treatments were assigned in the same random fashion as described in the field experiment. Seedling establishment, growth (seedling height and biomass), and survival were measured after sowing 30 seeds per tray at the time of soil treatment additions (25 July 2000). Sown seeds were pressed lightly into the soil surface in a similar fashion as in the field experiment. Eighty days after sowing (15 October 2000), established *Paspalum* and *Phytolacca* seedlings were thinned at random to six individuals or less per tray (depending upon establishment), measured for height, and marked for future measurements. Three seedlings per tray were harvested at random 160 d after sowing (on 2 January 2001), and the remaining three seedlings were harvested 245 d after sowing (on 28 March 2001). All seedlings thinned and harvested were chosen at random, and

percent survival, height, and total biomass were calculated similarly to those in the field experiment.

### Statistical Analysis

Soil N-mineralization,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were analyzed in a mixed-model doubly-multivariate repeated-measures MANOVA (SAS Institute, 1996), where the five soil treatments were fixed effects and the five landslide sites were random effects. This analysis is appropriate because there is one within subject factor (i.e., time) representing 45 and 360 d sampling, and more than one related response variable (von Ende, 1993). The laboratory incubation for N-mineralization was analyzed using a mixed model two-way ANOVA.

Time zero measurements (before amendments) were subtracted from all subsequent field sampling periods for SOM (LOI method), total N, available P, total P, pH, and soil moisture prior to analysis in order to account for within landslide variability. These soil variables were then analyzed in a mixed-model doubly-multivariate repeated-measures MANOVA (SAS Institute, 1996), where the five soil treatments were fixed effects and the five landslide sites were random effects. Soil bulk density and the  $\text{H}_2\text{O}_2$  method of SOM determination were analyzed using separate mixed model two-way ANOVAs. Screen-house soils were analyzed using a MANOVA with all variables (i.e., SOM, total N, available P, total P, pH, soil moisture) in one model for the single sampling period where the five soil treatments were fixed effects.

For the decomposition experiment, remaining biomass of *Cecropia* and *Cyathea* were analyzed for 60, 150, 300, 360 d sampling periods using a mixed-model repeated-measures MANOVA where the two litter treatments were fixed effects and the five

landslide sites were random effects. Foliar N and P at 370 d after litterbag additions were compared between *Cecropia* and *Cyathea* with mixed model two-way ANOVAs. Initial *Cecropia* and *Cyathea* litter and foliar pH were compared using t-tests.

For the field experiment, percent seed germination was analyzed for each species with a mixed model two-way ANOVA. Seedling establishment 80 d after sowing seeds was analyzed using a non-parametric Kruskal-Wallis test using JMP (JMP, 2000) after assumptions of normal distributions and equal variances were not met. Seedling height and biomass for *Paspalum* were analyzed in a mixed model doubly-multivariate repeated-measures MANOVA. Because of high mortality for *Phytolacca* seedlings, biomass, height, and survival were not statistically analyzed. Percent seedling survival was analyzed only for *Paspalum* using a mixed model two-way ANOVA after arcsin square-root transformation to meet assumptions of normality and equal variance.

For the screen-house experiment, seedling biomass and height for *Paspalum* and *Phytolacca* were analyzed in separately for each species using doubly-multivariate repeated-measures MANOVAs. Seedling establishment 80 d after sowing seeds was analyzed with a non-parametric Kruskal-Wallis test using JMP (JMP, 2000). Percent seedling survival was analyzed for *Paspalum* and *Phytolacca* using separate two-way ANOVAs for 160 and 245 d after seed sowing.

For all analyses, significant ( $P < 0.05$ ) multivariate comparisons, determined by Wilks' Lambda 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 (Steel & Torrie, 1980; Milliken & Johnson,

1992) was also performed when a significant ( $P < 0.05$ )  $F$  value was found. All analyses other than seedling establishment used General Linear Models procedures of SAS (SAS Institute, 1996), 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 treatment differences over the five different sites. Therefore, significant treatments and significant site x treatment interactions were the focus of this study.

## Results

### Soil Amendments

At the onset of the experiment, soil treatment quantities were determined based on total N concentrations from the literature. Following treatment additions, forest soil, *Cecropia*, and *Cyathea* treatments were analyzed to determine the actual N concentrations of each soil treatment. The forest soil averaged 0.47% N, nearly identical to the average found by Heyne (2000). When converted to g N per area of small treatment trays, 0.37 g N was added to small trays in the form of forest soil, which is nearly equal to the estimated value of 0.38 g N used across all treatments. Actual *Cecropia* and *Cyathea* litter used in the treatment additions had lower N than estimated from past studies, as *Cecropia* litter averaged 0.92%, or 0.24 g N added to small trays, and *Cyathea* litter averaged 0.82% N, or 0.21 g N added to small trays.

### Field Soils

Site, treatment, and site x treatment interactions were significant when available N soil variables ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , N-mineralization) were averaged across the two sampling



periods (between-subjects; Table 2.2). When analyzed individually, soil  $\text{NO}_3^-$  and soil N-mineralization had significant treatment effects, and N-mineralization had significant site x treatment interaction when averaged across time (Table 2.3). Averaged across all five landslides, available N soil variables showed significantly different treatment effects at different times (variable x time x treatment; Table 2.2). After 45 d, fertilizer-treated soils had a significantly higher N-mineralization rate than all other soil treatments ( $P=0.0002$ ; Fig. 2.2). Soil  $\text{NH}_4^+$  and  $\text{NO}_3^-$  followed the same pattern as N-mineralization, as fertilizer was significantly higher than all other treatments after 45 d for  $\text{NH}_4^+$  ( $P=0.0002$ ) and  $\text{NO}_3^-$  ( $P<0.0001$ ; Table 2.4), but concentrations were not different among treatments after 360 d (Table 2.4).

Significant site x treatment interactions were also present for N-mineralization ( $P=0.0003$ ) and  $\text{NH}_4^+$  ( $P=0.03$ ), indicating N-mineralization rates and  $\text{NH}_4^+$  were significantly different among landslides. N-mineralization in fertilizer plots was the lowest on the ES5 landslide 45 d after soil treatment (Fig. 2.3). Despite this, fertilized soils had the highest  $\text{NH}_4^+$  concentration after 45 d on ES5 (Fig. 2.4). The soil  $\text{NH}_4^+$  interaction appeared to result from the higher concentrations in the control and *Cecropia* treatments on landslides ES10 and J4 when compared to similar treatments on other landslides (Fig. 2.4).

The laboratory incubation experiment that took place *ca* 14 mo following treatment additions produced results similar to the field incubations after 360 d. Laboratory incubated soils were not significantly different among treatments for N-mineralization,  $\text{NH}_4^+$ , and  $\text{NO}_3^-$  ( $P>0.05$ ; data not shown).

In the field experiment there were no main effects of treatments, site, or treatment x site interaction when all soil variables (SOM, total N, available P, total P, pH, and moisture) were averaged across time (between-subjects treatment; Table 2.5). However, there was a highly significant interaction of variable x time x treatment (Table 2.5) indicating that different soil variable exhibited significant treatment responses in different individual sampling periods. Three of the soil variables did show consistent responses with significant treatment effects for SOM and pH and marginally significant total N averaged across time (Table 2.6).

Significant heterogeneity among landslides was present in this study, as soil variables differed among sites over time when all treatments were averaged (variable x time x site; Table 2.5). Despite the high site variability, significant site x treatment interactions were not present for any of the individual soil variables averaged across time (Table 2.6) nor during each individual time period (variable x time x site x treatment; Table 2.5). Therefore, treatment responses, when present, were consistent across all landslides.

To determine the treatment responses indicated by the significant variable x treatment x time interaction, I examined two-way ANOVA results for each time period for each soil variable (SOM, total N, available P, total P, pH, moisture). Soil variables were analyzed as differences from pre-treatment samples; however, the actual concentrations for the measured soil variables are also shown for each time period (Appendix Ia-c). The change from pretreatment soils by the addition of forest soil caused significantly higher SOM when compared to the control 60 d after soil treatment ( $P=0.04$ ; Fig. 2.5). After 210 d, SOM was significantly higher in *Cecropia* than in the control ( $P=0.04$ ; Fig. 2.5). Compared to pretreatment soils, soil total N was higher in plots amended with forest soil

after 60 d compared to controls ( $P=0.03$ ; Fig. 2.6). Only fertilized soils had significantly higher available P than the control after 60 d ( $P=0.003$ ; Fig. 2.7). Despite no treatment differences after 60 d, total P in the control treatment was significantly higher than pretreatment soils compared to those of *Cecropia* 210 d after soil treatment addition ( $P=0.04$ ), and total P levels were not significantly different among treatments during other time periods (Fig. 2.8).

Soil pH (difference from pretreatment values) changed significantly through time for each treatment and followed the same general trend across all treatments. Soil pH dropped between the 60 and 210 d sampling periods and then increased. Fertilizer caused soil pH to drop significantly lower than all other soil treatments after 60 d ( $P<0.0001$ ; Fig. 2.9). At 210 d, pH of fertilizer and forest soils were significantly lower than *Cecropia* ( $P=0.004$ ), and after 370 d forest soil was significantly lower than *Cecropia* ( $P=0.04$ ; Fig. 2.9). Soil moisture (difference from pretreatment) was not significantly different among treatments for any of the sampling periods ( $P=0.62$ ,  $P=0.62$ ,  $P=0.95$ , for 60, 210, and 370 d, respectively). Similarly, soil bulk density, measured only at 370 d after treatment addition, was not significantly different among soil treatments ( $P=0.11$ ).

Soil texture was significantly different among landslide sites. The two landslides with Inceptisols (RB10, MY8) had significantly higher sand ( $P<0.0001$ ) and lower clay ( $P<0.0001$ ) than the Ultisol landslides (Fig. 2.10). The order in which landslides differed significantly with respect to sand was: RB10 & MY8 > J4 & ES5 > ES10. Clay percent followed the reverse order: ES10 > J4 & ES5 > RB10 & MY8. Percent silt was significantly higher ( $P=0.03$ ) on landslides J4 & ES5 compared to RB10. The Ultisols

from landslides ES10, ES5, and J4 are sandy clay loams; whereas the Inceptisols from landslides RB10 and MY8 are loamy sands.

The H<sub>2</sub>O<sub>2</sub> method for determining SOM for the August 2000 soils revealed SOM concentrations were not significantly different among treatments (P=0.06), and values were substantially lower than those using the LOI method. While LOI means ranged from 5.54% to 17.29% (avg. 11.85%; Appendix 1c) for the August 2000 sampling period, means for each treatment using the H<sub>2</sub>O<sub>2</sub> method tended to be highest for forest soil (1.70%), followed by *Cecropia* (1.69%), control (1.32%), *Cyathea* (1.20%), and fertilizer (0.73%).

### Decomposition

A significant treatment effect for litter decomposition was found from the repeated-measures MANOVA when averaged across time (between-subjects) and through time (time x treatment), as well as an interaction (time x site x treatment; Table 2.7). Results of the year-long decomposition experiment showed *Cyathea* decomposed significantly faster than *Cecropia* leaf-litter during each sampling period (P<0.03 for each period; Fig. 2.11). Additionally, there was a site x treatment interaction for 60 d (P<0.0001) and 150 d (P=0.04) after 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 (Fig. 2.12), whereas after 150 d, the significant interaction appeared to result from low values for *Cecropia* on the RB10 landslide (Fig. 2.13).

Undecomposed *Cecropia* litter had approximately 1 mg N per g more than undecomposed *Cyathea* litter initially (df=4; P=0.03). Interestingly, *Cecropia* litter that decomposed on landslides for one year had a similar N concentration as undecomposed

*Cecropia*, but *Cyathea* N decreased by approximately 50% (Table 2.8). When foliar N and P were compared between *Cecropia* and *Cyathea* after one year of decomposition, *Cecropia* had significantly higher N than *Cyathea* ( $P < 0.0001$ ). However, this was not the case with remaining P, as total P was similar initially and after one year when *Cecropia* and *Cyathea* were compared ( $P > 0.05$ ; Table 2.8). Finally, there was a site x treatment interaction for total N ( $P = 0.05$ ) supported by a lack of treatment difference on landslide J4 (Fig. 2.14). Although *Cecropia* ( $5.267 \pm 0.006$ ) had a slightly higher pH than *Cyathea* ( $5.167 \pm 0.001$ ), foliar pH was not significantly different between species ( $P = 0.10$ ;  $df = 4$ ).

#### Screen-house Soils

A significant soil treatment effect was present in the screen-house experiment MANOVA when SOM (LOI method), total N, available P, total P, pH, and moisture were averaged (Num. d.f.=24, Den d.f.=106,  $P < 0.0001$ ). After one year following soil treatment, forest soil SOM was significantly higher than all other treatments in the screen-house experiment, and *Cecropia* and *Cyathea* had significantly higher SOM than fertilizer and control treatments ( $P < 0.0001$ ; Fig. 2.15a). Forest soil had significantly higher total N than all other soil treatments, and *Cecropia*, but not *Cyathea*, had significantly higher total N than fertilizer and control treatments ( $P < 0.0001$ ; Fig. 2.15b). Neither soil available P nor total P were significantly different when soil treatments were compared in the screen-house experiment ( $P > 0.05$ ). Fertilizer, followed by forest soil, had significantly lower soil pH than all other treatments ( $P < 0.0001$ ; Fig. 2.15c). Soil moisture was significantly higher in *Cyathea* when compared to fertilizer ( $P = 0.02$ ; Fig. 2.15d). Landslide soils used in the screen-house experiment were classified as clay using USDA texture triangle (sand:  $15.9 \pm 1.1\%$ ; silt:  $34.1 \pm 0.4\%$ ; clay:  $50.0 \pm 1.4\%$ ).

### Field Plant Responses

Fertilizer significantly enhanced the percent of *Paspalum* seeds that germinated in the field experiment when compared to *Cecropia* soils ( $P=0.05$ ), yet no other treatments significantly altered *Paspalum* germination (Fig. 2.16). There were no differences in *Phytolacca* germination across all five treatments ( $P>0.05$ ), and there were no site x treatment interactions for either seed type ( $P>0.05$ ), although *Paspalum* germination was two fold higher than *Phytolacca* germination. Despite a treatment difference in seed germination for *Paspalum*, there were no significant treatment differences for either *Paspalum* or *Phytolacca* for seedling establishment 80 d after seed sowing. Moreover, *Paspalum* seedling biomass was not different between soil treatments 235 d after sowing ( $P>0.05$ ), though seedlings in fertilizer tended to have the highest biomass (fertilizer  $556.5\pm 247.5$ ; forest soil  $260.2\pm 110.4$ ; control  $176.7\pm 79.1$ ; *Cecropia*  $140.2\pm 63.1$ ; *Cyathea*  $133.4\pm 35.2$  mg). Survival of *Paspalum* seedlings at 235 d was high ( $>80\%$ ), and seedlings sown in *Cyathea* had significantly greater survival than those sown in controls ( $P=0.01$ ; Fig. 2.17). *Phytolacca* seedlings in control or *Cyathea* soil did not survive to 235 d after sowing, and *Phytolacca* seedling mortality was high across all treatments ( $<20\%$ ) such that samples sizes after 235 d were too small to analyze statistically (Fig. 2.17).

### Screen-house Plant Responses

Results of the MANOVA models for seedling biomass and height for the screen-house experiment suggest a significant treatment effect averaged across time (between-subjects) and through time (within subjects) for both *Paspalum* (Table 2.9) and *Phytolacca* (Table 2.10). Fertilizer, followed by forest soil, had significantly higher

*Paspalum* seedling biomass during all three sampling periods ( $P < 0.0001$ ; Fig. 2.18). There were no significant biomass differences among *Cecropia*, *Cyathea*, and control treatments ( $P > 0.05$ ; Fig. 2.18). Similar results were found for *Phytolacca* seedling biomass (Fig. 2.19). However, for *Phytolacca* seedlings, there were too few survivors in the *Cecropia*, *Cyathea*, and control treatments for analysis at 245 d. Seedling heights followed similar overall patterns as biomass for *Paspalum* ( $P < 0.0001$ ; Fig. 2.20) and *Phytolacca* ( $P < 0.0001$ ; Fig. 2.21), with the exception that *Paspalum* seedlings were significantly shorter in *Cecropia* and *Cyathea* treatments when compared to the control after 80 and 160 d following soil treatment (Fig. 2.20).

Seedling establishment, measured as the number of seeds that germinated and survived to 80 d following seed sowing, was not significantly different among treatments in the screen-house experiment for either *Paspalum* or *Phytolacca* ( $P > 0.05$ ). After 160 d, average percent survivorship for *Paspalum* and *Phytolacca* seedlings in the screen-house experiment was  $> 80\%$  (Fig. 2.22) and there were no significant differences among treatments for either *Paspalum* or *Phytolacca*. *Paspalum* seedling had a higher overall survivorship when compared to *Phytolacca* seedlings after 245 d, and *Paspalum* seedlings in forest soil and fertilizer treatments were significantly higher than in all other treatments ( $P < 0.0001$ ). Seedling results for *Phytolacca* were more severe after 245 d, as seedlings sown in *Cecropia*, *Cyathea*, and control treatments all died. Although fertilized soils tended to have a higher percentage of surviving *Phytolacca* seedlings compared to forest-amended soils after 245 d, there was not a significant difference between these two treatments ( $P = 0.09$ ). Overall, *Paspalum* and *Phytolacca* seedlings grown in forest soil or fertilizer-treated soil survived best after 245 d (Fig. 2.22).

## Discussion

### Field Soils

This study showed that soil properties (without soil treatment alteration) differed widely among the five landslides in the Luquillo Experimental Forest. Soil particle size reflects the marked differences among landslides and supports the previous distinction of landslides into two soil orders. However, most measured soil variables varied independently of soil orders (data not shown). Despite the high variation in the soil characteristics among sites, as well as leaching and harsh environmental conditions that are characteristic of landslides in general, treatment differences across the five different landslides were consistent for nearly all individual soil variables. These results reinforce the assumption that nutrients are limiting on tropical landslides (Walker et al., 1996), and that organic matter and fertilizer alter soil fertility on landslides in the LEF despite the high variation of soil nutrients across small spatial scales common to tropical forests (Ewel et al., 1981, 1991; Silver et al., 1994, 1996).

Soil chemical and physical properties were altered from initial, untreated landslide soils in the LEF by application of *Cecropia* leaves, *Cyathea* fronds, forest soil, and fertilizer. No single treatment altered all of the measured soil variables. Fertilizer and forest soil additions had the largest effects during the initial 60 d (Fig. 2.23). Following 60 d, fewer treatment effects were present, as there were only two soil variables (total P and SOM) that showed significant treatment effects at 210 d and there was an absence of treatment effects among all of the measured soil variables at 370 d. The lack of significant treatment effects as time progressed was likely due to treatment and nutrient loss from leaching, sorption, and biotic uptake. Therefore, despite the addition of



nutrients in the form of fertilizer and organic matter to landslide soil in the LEF, short-term (60 d) increases in soil fertility appears to be produced only by the addition of fertilizer (increasing both available N and available P) and forest soil (increasing total N and SOM). *Cecropia* increased SOM at 210 d and *Cyathea* did not produce any positive soil fertility effects over the year-long experiment, suggesting the type and stage of decomposition that the organic matter is in is important for soil fertility in landslides within the LEF.

The increase in available N and available P following addition of fertilizer suggests that this soil amendment is the best for plant growth in the short-term (60 d). The lack of significant increases for the remaining treatments suggests that available nutrients are bound up in organic matter and not easily released, or that microbial uptake consumed available nutrients in the presence of a carbon source. While both  $\text{NH}_4^+$  and  $\text{NO}_3^-$  significantly increased when fertilizer was added, the majority of available N present at 60 d was in the form of  $\text{NO}_3^-$ . This result is contrary to the findings of a landslide fertilization experiment by Fetcher et al. (1996), where  $\text{NH}_4^+$  was the highest available source of N. The difference between these studies may be due to higher rates of nitrification in my study, or simply that 38% more  $\text{NH}_4^+$ -based fertilizer ( $27 \text{ g N m}^{-2}$ ) was used by Fetcher et al. (1996) than in my study ( $19.5 \text{ g N m}^{-2}$ ). Although  $\text{NH}_4^+$  is less energetically expensive for plants to utilize compared to  $\text{NO}_3^-$ , most plants rely on  $\text{NO}_3^-$ , and  $\text{NH}_4^+$  can be toxic in high doses (Sprenst, 1987). However,  $\text{NO}_3^-$  is soluble and easily leached, which may explain the decrease in available N after 60 d.

Nitrogen-mineralization, which is largely a measure of microbial activity, also increased in the commercial fertilizer treatment during 45-60 d time period (14 d

incubation) compared to all other treatments. This result suggests that nutrients are more limiting to microbes than carbon in these landslide soils. The lack of treatment effects during the 360 d sampling for N-mineralization,  $\text{NH}_4^+$ , and  $\text{NO}_3^-$ , and the laboratory incubation (data not shown) suggests that N in fertilizer was quickly lost. Microbial activity (measured as N-mineralization) is low in these landslide soils, as control treatment averages ( $0.03 \text{ g N mo}^{-1}$ ) were more than one order of magnitude lower than control soils in the forest understory in the LEF (*ca*  $0.5 \text{ g N mo}^{-1}$ ; Zimmerman et al., 1995). Microbial biomass has been shown to increase with landslide age and development in the LEF (H. Ruan, unpublished data), which further supports the lack of significant microbial activity on these five young landslides. Significant microbial immobilization was not found in this study, which contrasted with previous studies where carbon was added to soil in temperate grasslands (Reever Morghan & Seastedt, 1999), temperate scrub (Zink & Allen, 1998), or mature subtropical forest (Zimmerman et al., 1995). However, *Cecropia* and *Cyathea* treatments tended to have  $\text{NH}_4^+$  and  $\text{NO}_3^-$  averages slightly lower than controls when compared at the 45 d time period, suggesting some of the nutrients released during decomposition of leaf litter were utilized by the few microbes present, therefore leaving slightly less available N for plant uptake.

Forest soils containing organic matter and foliar material of both *Cecropia* and *Cyathea* clearly have substantial amounts of organic carbon. However, after 60 d, only the forest soil treatment showed a significant increase in SOM when compared to the control. This was likely the result of a higher initial concentration of organic matter  $<2 \text{ mm}^2$  in the forest soil treatment than the *Cecropia* and *Cyathea*. Higher SOM in *Cecropia*-treated soils compared to the control after 210 d can be explained by the slow

decomposition of this species (compared to *Cyathea*), causing it to persist in the soil for a greater length of time (see decomposition discussion). The absence of a SOM treatment effect after 370 d may explain why soil bulk density was not different across treatments after one year. Significant organic matter, if present, would have decreased bulk density.

Total soil N in the forest soil treatment was significantly greater than in control soils after 60 d, indicating the link between high total N concentrations in soils treated with a higher concentration of organic matter. The higher SOM and total N are beneficial conditions for plant growth (Kielland, 1994; Chapin, 1995) suggesting forest soil may be a helpful soil amendment for landslide revegetation. Unlike SOM results, total N values did not differ for the remaining treatments during the course of the experiment. This is particularly interesting in the case of *Cecropia* as it had a higher SOM concentration after 210 d and a high foliar N concentration of *Cecropia* leaves was recorded at the end of the 1 yr decomposition experiment. The absence of an increase in total N in fertilized soils at the 45-60 d period despite an increase in available N confirms that the plant available N pool is small and disappears quickly (Binkley & Vitousek, 1989). Total soil N concentrations before treatment additions averaged 0.02% in this study (see Appendix Ia), which was substantially less than forest soil concentrations in a past study in the LEF (0.37%; Guariguata, 1990); but within the range of previous landslide studies in the LEF, as TKN averaged 0.05% in upper portions of landslides in one study (Guariguata, 1990), and between 0.04% to 0.09% in slightly more developed portions (e.g., higher organic matter concentrations) of other LEF landslides (Walker, 1994).

Available P is low in landslide soils in the LEF compared to soils under the forest understory (Guariguata, 1990; Myster & Fernández, 1995). Concentrations in my study

( $2.1 \mu\text{g g soil}^{-1}$ ; see Appendix Ib) were nearly identical to concentrations in the upper portions of landslides in the LEF found by Guariguata (1990;  $2.0 \mu\text{g g soil}^{-1}$ ), and slightly higher than labile P concentrations ( $1.37 \mu\text{g g soil}^{-1}$ ) in <5 yr old landslides in the LEF found by Frizano et al. (2002). On an areal basis, my values (mean:  $0.007 \text{ g m}^{-2}$ ; range:  $0.0006\text{-}0.026 \text{ g m}^{-2}$ ) were substantially lower than concentrations in 6-20 year old LEF landslides (Myster & Fernández, 1995; mean:  $0.108 \text{ g m}^{-2}$ ; range:  $0.015\text{-}0.521 \text{ g m}^{-2}$ ). Caution should be taken in comparing the available P between these studies, as the extraction methods were different. Fertilizer significantly increased available P after 60 d compared to all treatments except *Cyathea* soils. This finding contrasts with the conclusion of Frizano et al. (2002) who suggested that increased available P was due mainly to higher litter inputs based on increased soil carbon correlating with available P in LEF landslides. Nevertheless, fertilizer containing P can increase the concentration of available P on landslides in the LEF in the short-term (Fetcher et al., 1996; this study).

Total soil P was not increased by any of the organic matter additions in this study. This suggests that any P converted to available forms by microbial activity was quickly lost from the soil. Average concentrations of total P were similar in this study ( $0.25 \text{ mg g soil}^{-1}$ ; see Appendix Ia) to that of Guariguata (1990) in the upper landslide zone ( $0.25 \text{ mg g soil}^{-1}$ ), and slightly lower than that of Walker (1994) on landslides covered by climbing ferns ( $0.4\text{-}0.6 \text{ mg g soil}^{-1}$ ). Despite the study by Walker (1994) having more total P on an older landslide, past studies in the LEF suggest that total P does not change with increased soil development (Guariguata, 1990; Zarin & Johnson, 1995). However, my study showed a pulse of total soil P at 210 d in the control treatment, which is likely the result of two related scenarios. First, weathering of the newly exposed substrate that had

been mixed *in situ* could have increased the release of P. The main source of soil P is bound in the parent material, and is released through physical and mechanical weathering processes (Walker & Syers, 1976; Newman, 1995; Schlesinger, 1997; Foth & Ellis, 1997). Secondly, soil biota in the four amended soil treatments may have utilized newly released P or converted P into soluble forms more susceptible to leaching, thereby causing the absence of a change in total P for these treatments at the 210 d time period. Past studies of soil P on landslides in Puerto Rico (e.g., Guariguata, 1990; Walker, 1994; Myster & Fernández, 1995; Zarin & Johnson, 1995) have not accounted for temporal changes within a given site, as single sampling dates are the norm. Therefore, short-term, temporal changes, especially following soil disturbance, may be more common than previously believed (Silver et al., 1996), and this is supported by the increase in total P in control treatments for the single time period.

Soil pH directly affects soil microorganisms and the availability of plant nutrients (Sparks, 1995; Sollins, 1998). Soil pH was decreased in two ways in this study. First, the commercial fertilizer treatment significantly lowered pH below all other treatments at the 60 d sampling, and was significantly lower than *Cecropia* soil at the 210 d sampling. Adding  $\text{NH}_4^+$ -based fertilizer generally decreases soil pH (Sparks, 1995; Foth & Ellis, 1997) as  $\text{NO}_3^-$  and  $\text{H}^+$  ions are formed when  $\text{NH}_4^+$  is oxidized. This may also partly explain the significant increase in  $\text{NO}_3^-$  and minimal increase in  $\text{NH}_4^+$  at the 60 d sampling described earlier. Secondly, adding organic matter also decreases soil pH as  $\text{H}^+$  ions are added to the soil through decomposition (Jenny, 1980; McLean, 1982; Sparks, 1995). This was shown with the forest soil treatment, which had high SOM initially and decreased pH levels after 210 d and 370 d compared to *Cecropia*-treated soils, which

decomposed slowly. Interestingly, all soil treatments (including the control) followed the same general trajectories in soil pH through time, as values dropped between the 60 d and 210 d time period, and returned to values more-closely related to 60 d sampling after 370 d. This collective drop in pH could be the result of mixing the soil *in situ* as bioturbation is known to lower pH values (Foth & Ellis, 1997), or a response to seasonality as the 270 d period occurred in the slightly drier season in the LEF. Sollins (1998) noted radical changes in soil pH at 6 mo and 12 mo periods in disturbed and undisturbed portions of a lowland tropical rain forest, and Silver et al. (1996) found soil pH decreased in both disturbed and undisturbed sections of the LEF following a drought.

Figure 2.23 summarizes the soil responses to the field treatment additions over the course of the 1 yr experiment and can therefore help in the understanding of the biogeochemical effects of organic matter and fertilizer inputs to landslides in the LEF. This model shows that soil treatments in LEF landslides are most effective up to 210 d, as treatment effects are absent at 370 d. Despite organic matter containing nutrients, only forest soil showed initial (60 d) positive effects (increasing total N and SOM) on soil fertility, whereas *Cecropia* increased SOM at 210 d, and *Cyathea* did not show any positive effects on soil fertility throughout the experiment. Fertilizer application increased plant available N and P at 60 d. Therefore, “natural” inputs of forest soil from landslide edges, and anthropogenic application of fertilizer appear to have the greatest positive effect on increasing soil fertility in landslides within the LEF.

### Decomposition

Rates of decomposition and foliar nutrient loss determine soil fertility and are important for supplying soil nutrients for plant growth. Temperature, moisture, and soil

conditions often affect decomposition (Bloomfield et al., 1993; González & Seastedt, 2001), and these characteristics may help explain differences in decomposition among landslides at two of the four time periods. *Cyathea* decomposed more quickly on landslide ES5 after 60 d, and *Cecropia* decomposed at a higher rate on RB10 after 150 d. Overall, *Cyathea* decomposed 10% faster than *Cecropia* when averaged across all landslides and sampling dates. This may be due to a combination of high lignin content of *Cecropia* leaves causing slower decomposition, as well as a more rapid decay of the pinnae of *Cyathea* fronds. *Cyathea* decomposition and foliar information is unavailable; however, remaining *Cecropia* biomass in this study (88% after 65 d; 53% after 1 yr) was similar to past *Cecropia* studies in the forest understory in the LEF (80% after 65 d; La Caro & Rudd, 1985; ca 40%; ca 65% with macroinvertebrates excluded after 1 yr; González and Seastedt, 2001). The slightly higher retained *Cecropia* biomass in my study compared to the other two studies is likely due to the lower microbial biomass on landslides in the LEF compared to the forest understory (H. Ruan, unpublished data).

Although N has been described as a good predictor of plant litter decomposition (Melillo et al., 1982; Coûteaux et al., 1991), it does not apply to this study because *Cecropia* had higher initial and ending (after 1 yr decomposition) foliar N concentrations compared to *Cyathea*. However, several studies have shown that lignin content has more control than N over decomposition rates (Bollen, 1953; Singh, 1969; Fogel & Cromack, 1977; La Caro & Rudd, 1985; Bloomfield et al., 1993). In contrast to plant compounds such as cellulose, lignin is relatively resistant to decay and there are only a few microorganisms known that can break it down (Higuchi, 1985; Swift et al., 1979). *Cecropia* leaves from the LEF have high lignin content, where only *Inga vera* leaves had

a higher lignin concentration than *Cecropia* among six common plant species studied within the LEF (La Caro & Rudd, 1985). Carreiro et al. (2000) found that leaves containing high lignin suppressed lignin-degrading phenol oxidase activity and therefore slowed decomposition when exogenous N was applied, yet leaves with low lignin degraded significantly more quickly. The high lignin content previously reported for *Cecropia*, as well as the high and persistent N concentration of *Cecropia* compared to *Cyathea*, supports the possibility that lignin-degrading phenol oxidase activity may be suppressed in *Cecropia* leaves. In contrast, the lignin content of *Cyathea* is not known, but the rachis is believed to have high lignin (woody outside surface) and the pinnae are thought to have low lignin (J. Lodge, personal communication). Therefore, the more rapid decomposition of *Cyathea* may be due mostly to the decay of the pinnae portions of the fronds. Despite the quicker decomposition and greater foliar N released from *Cyathea* litter, soil nutrient data suggests that *Cyathea* litter is not helpful as a supply of nutrients to landslide soils. Although *Cecropia* minimally altered landslide soils during the year experiment, the possibility of facilitative effects on soil fertility by further decomposition of *Cecropia* may appear at a later time period.

#### Screen-house Soils

Unlike the field experiment, the screen-house experiment did not track soil responses to treatments through time, as the main purpose of the screen-house soil sampling was to help explain plant responses to the soil treatments in the screen-house. A major difference in soil responses between the screen-house and the field experiment was temporal, as all treatment effects in the field experiment were at 60 d and 210 d, and no treatment effects existed at 370 d. The confinement of the soils in trays in the screen-



house may have contributed to different rates of leaching between the screen-house and landslides. However, a more likely explanation for the presence of soil treatment effects in the screen-house while absent on the landslides after one year can be explained by the marked difference in clay content of the screen-house soils (50%) compared to the landslides (range: 4-36%). More colloid surface area and higher cation exchange capacity (CEC) are characteristic of clay soil particles (Sparks, 1995; Foth & Ellis, 1997). Therefore, clay soils retain more nutrients and water, whereas lower clay soils (i.e., field experiment) are more likely to lose nutrients and water at an accelerated rate. Despite the temporal difference in soil sampling between the screen-house and the field experiment, responses to soil treatments were similar, reinforcing the general ability of the effects of the soil amendments on soil conditions.

Similar to clay, the presence of SOM increases soil colloids and therefore retains more nutrients (Sparks, 1995; Foth & Ellis, 1997). Forest soil had higher SOM and total N in the screen-house experiment, which was a similar pattern to that present at 60 d in the field experiment. However, one year concentrations of total N in forest soil treatments tended to be higher in the screen-house experiment ( $706.4 \mu\text{g g soil}^{-1}$ ) than in the field experiment ( $444.2 \mu\text{g g soil}^{-1}$ ). *Cecropia* and *Cyathea* also had higher SOM than fertilizer and control treatments in the screen-house, but only *Cecropia* had higher concentrations of total soil N, reflecting the difference in decomposition between these two litter treatments. Unlike forest soil, total N averages for remaining treatments were similar for both the field and screen-house (see Appendix Ia; Fig. 8).

Substantial nutrient loss was also evident in the screen-house experiment, as all nutrient measurements in fertilizer were similar to the controls after one year, and there

were no differences among treatments for available P and total P. However, soil pH treatment effects in the screen-house reflected those in the field. Fertilized soil had the lowest pH, followed by the forest soil treatment, supporting the previously described conclusions in the field experiment where  $\text{NH}_4^+$ -based fertilizer and decomposition of organic matter decrease soil pH. However, *Cecropia* and *Cyathea* did not differ from the control in soil pH, suggesting that decomposition is occurring at a different rate in the screen-house than in the field, or that the high clay soils in the screen-house have a larger buffering capacity to house  $\text{H}^+$  on exchange sites.

Soil moisture was also likely affected by the water-retention properties of clay, as soils in the screen-house tended to have much higher soil moisture among all treatments (range: 74-83%) than those of the field across all sampling periods (range: 27-68%; see Appendix 1c). Although *Cyathea* had significantly higher soil moisture than fertilizer in the screen-house, the difference among all treatments was minimal, as organic matter treatments ranged from 79-83%, whereas the control and fertilizer had 75% and 74%, respectively. Therefore, the slight differences between *Cyathea* and fertilizer treatments are not likely to significantly affect nutrients or plants.

#### Field Plant Responses

The grass species, *Paspalum millegrana*, responded to the commercial fertilizer treatment in the field experiment by exhibiting higher germination than in *Cecropia*-treated soil across all landslides. This finding reflects the results of the nutrient analyses in the field experiment, bench experiment, and the decomposition experiment, as *Cecropia* decomposes slowly and retains the majority of its N in the foliar material longer than all other organic matter treatments. Although results of N incubations suggest N-

immobilization was not a substantial factor in this study, each of the organic matter additions tended to reduce average germination slightly below the control, and this trend matched that of *Cecropia*- and *Cyathea*-treated soils having slightly lower  $\text{NH}_4^+$  and  $\text{NO}_3^-$  after 45 d following treatment additions.

The high germination success of *Paspalum*, even without the addition of fertilizer may facilitate revegetation on landslides, but inhibit forest succession over the long-term as grasses commonly dominate landslides and persist for decades in both the LEF (Walker & Boneta, 1995; Walker et al., 1996) and in Hawaii (Restrepo & Vitousek, 2001). Therefore, caution should be taken if utilizing fertilizer in future restoration to facilitate forest succession rather than revegetation of landslides in the LEF based on these germination results, and the observations that landslides (especially those <5 yr old) are dominated by seed rain attributed to grasses (see Chapter 1).

Germination of *Phytolacca rivinoides*, a large pioneer herb, did not respond to fertilizer addition, and seed germination was not different among treatments. This result is different from Fetcher et al. (1996) where additions of fertilizer stimulated the existing seedbank of *Phytolacca rivinoides* on a 19 mo old landslide in the LEF (L. Walker, personal communication; J. Lodge, personal communication). However, the positive result in their study could have been due in part to disturbing the soil (digging and back-filling a 60 cm trench between treatment rows), thereby exposing an existing *Phytolacca* seedbank (which can remain dormant for >27 mo at 15 cm soil depth; Murray, 1988) to light. *Phytolacca* had higher germination success in high than low light environments in Costa Rica (Murray, 1988). Germination of *Phytolacca* in a shade-house in the LEF (Walker and Neris, 1993) was higher (38-70%) than in the higher light environment on

landslides in my study (30%), but this difference could have been a result of seed loss from overland flow on landslides. Although percent germination of *Phytolacca* was less than half that of *Paspalum* (76%), *Phytolacca* could be particularly important for accelerating plant succession because a single individual can grow to cover up to 25 m<sup>2</sup> within 1-2 yr of seedling establishment and produces between 1,500-30,000 multi-seeded fruits during a single fruiting season (Murray, 1988). Because *Phytolacca* is generally dispersed by birds (Murray, 1988; Devoe, 1989), facilitating the arrival of seeds into landslides may also be necessary to promote succession (see Chapter 1).

Seedling establishment, measured in the field after 80 d following seed sowing, was not different among treatments for either *Paspalum* or *Phytolacca*. This suggests there was a higher mortality of *Paspalum* seedlings between the germination and establishment stage in fertilized soils to compensate for the significantly higher seed germination in fertilized soils. It is probable that substantial treatment loss occurred from the time since initial soil treatment and seed sowing for seedling establishment (*ca* 120 d), and this may explain the lack of treatment effects for both species. Although *Paspalum* seedling survival was higher in *Cyathea* than in the control after 235 d, *Paspalum* survival was higher for all treatments after 235 d (>80%) compared to *Phytolacca* (7.7% for all treatments), suggesting that the grass is a better colonist on landslides compared to the large herb.

Forest soil and fertilizer increased soil fertility initially (60 d) and accounted for the majority of the *Phytolacca* seedlings surviving to 235 d. This suggests that soil nutrients are at least in part critical to *Phytolacca* seedling survival, and the timing of nutrient availability may also be critical. Specifically, *Phytolacca* seedlings may be limited by

soil P as evident by the following: soil P is low on these landslides, Fetcher et al. (1996) found *Phytolacca* seedlings the most responsive of four plant species to P fertilizer on landslides, and *Phytolacca* is nonmycorrhizal (Janos, 1980; Calderón-González, 1993). Low densities of mycorrhizae in disturbed soils have been proposed as a limitation to plant growth in the tropics (Janos, 1980; Cuenca & Lovera, 1992) and specifically in landslides in the LEF (Myster & Fernández, 1995). In contrast to *Phytolacca*, mycorrhizae are not likely to contribute to the persistence of *Paspalum* survival, as it has a denser and finer root system that is typical of most grasses, and therefore is probably not dependent on mycorrhizae as a source of P (Cooperband et al., 1994; Salinas et al., 1985).

Based on the seed, seedling, and survivorship results from the field experiment, I conclude that the fertilizer treatment facilitates *Paspalum* but not *Phytolacca* germination in the LEF and that *Paspalum* seedling growth and survival are less affected by low nutrient conditions than seedlings of *Phytolacca*. The nutrient limitation for *Phytolacca* seedlings on landslides in the LEF was shown by Fetcher et al. (1996) when fertilizer was added every 3 mo for one year. With high inputs of seed rain, high germination success, and extended survival, even in unfertilized soils, *Paspalum* is likely to colonize landslides quickly and persist for extended periods of time. In contrast, these results suggest colonization of landslides by *Phytolacca* is limited by nutrients, and *Phytolacca* individuals colonizing disturbed areas such as landslides are likely optimizing nutrient patches in the soil.

### Screen-house Plant Responses

The timing of available soil nutrients for both *Paspalum* and *Phytolacca* appear to be critical to growth and survival. Unlike the field experiment, where a seed germination experiment took place before the reseeding of treatment trays for seedling establishment and growth measurements, soil treatments were added simultaneously with sowing seeds in the screen-house experiment. The delayed seeding for these measurements, as well as the difference in soil clay content, could account for the lack of seedling treatment effects and the high mortality in the field experiment when compared to the screen-house experiment. As shown with available N and available P in the field experiment, soil nutrients were quickly lost in the field experiment.

The most noticeable seedling response in the screen-house experiment was the increase in seedling biomass and seedling height for both *Paspalum* and *Phytolacca* in fertilized landslide soils when compared to all other treatments. *Paspalum* biomass in fertilized trays was 7-, 8-, and 10-fold higher than in control trays after 80 d, 160 d, and 245 d, respectively. *Phytolacca* biomass in fertilized trays was 4- and 8-fold higher than in control trays after 80 d and 160 d, respectively. The presence of this same response for both seedlings supports conclusions of past studies, both in the LEF (Guariguata, 1990; Fetcher et al., 1996) and in Jamaica (Dalling & Tanner, 1995), that nutrients are limiting to plant growth in landslide soils.

*Paspalum* and *Phytolacca* seedling biomass and height showed an intermediate growth response (between the control and fertilizer treatment) in forest soil treatments that correlates with high soil nutrients compared to other treatments. Forest soil is likely a higher quality organic matter than leaf litter (e.g., from *Cecropia* or *Cyathea*), and soils

from the forest understory in the LEF have higher microbial biomass than soils from recent landslides (H. Ruan, unpublished data). Therefore, the facilitative effects of forest soil on seedling growth found here supports past studies suggesting that remaining patches of forest soil in landslides provide more suitable sites for plant growth than areas where forest soil was removed (Guariguata, 1990; Walker et al., 1996).

*Cecropia* and *Cyathea* did not increase seedling growth in the screen-house experiment. Although *Cecropia* decomposes more slowly than *Cyathea*, there was not a significant difference in seedling biomass or height between these two treatments. Interestingly, *Paspalum* seedling heights were significantly decreased by additions of *Cecropia* and *Cyathea* leaves when compared to the control, which may be a result of nutrient immobilization by microbes, or physical inhibition due to litter in the rooting zone. Neither of these hypotheses were directly tested in the screen-house experiment. Significant N-immobilization did not occur in the field when these treatments were added to landslide soil *in situ*; however, *Cecropia* and *Cyathea* tended to have lower available N concentrations compared to the control at the first sampling. The presence of *Cecropia* and *Cyathea* litter (*ca* 1 cm<sup>2</sup>) in the soil may have also physically inhibited root growth causing a greater allocation of biomass to roots (Hutson & Smith, 1987; Tilman, 1988; Chiariello et al. 1989;). Although biomass is generally a better predictor of plant growth than height (Chiariello et al., 1989; Barbour et al., 1999) the decreased height of *Paspalum* seedlings support the inhibitory effect of *Cecropia* and *Cyathea* treatments on plant growth.

Seedling survival of *Phytolacca* was much lower than that of *Paspalum* in the screen-house experiment. All *Phytolacca* seedlings in the control, *Cecropia*-, and *Cyathea*-

treated soils died in the screen-house experiment after 245 d after sowing. *Phytolacca* seedlings survived best in fertilized soil, and slightly lower in forest soil, matching the seedling biomass and height data. *Paspalum* seedling survival also reflected the seedling biomass and height results, as seedlings suffered high (>50%) mortality in the control, *Cecropia*, and *Cyathea* treatments after 245 d, but survived well in fertilizer and forest soil (>80%).

Results of *Paspalum* and *Phytolacca* seedling biomass and height growth show that nutrients are limiting in the screen-house soils, and fertilizer and forest soil are helpful amendments to accelerate plant growth. Biomass and height growth of *Cecropia* and *Cyathea* were either similar to or less than the control, suggesting these two soil amendments do not aid in plant growth. With the exception of the forest soil treatment, soil nutrients did not predict seedling growth responses among treatments, but this was likely due to a single sampling after one year following treatment additions.

### Conclusion

Despite wide variation in landslide soil type, location in the LEF, and pre-treatment soil properties, additions of organic matter and fertilizer altered soil variables in a consistent pattern across the landslides used in this study. Seed and seedling dynamics were also altered by the soil treatments in both the field and screen-house experiments. Therefore, the nutrient limitation in landslide soils in the LEF affects soils, seeds, and seedlings of early-colonizing landslides species, and the additions of organic matter and fertilizer can positively affect landslide properties that influence plant succession across a wide range of soil conditions.



This study has shown both positive and negative effects of the soil treatments when they were applied to a wide range of landslide soils. Fertilizer caused the greatest positive response for both plants and soils as it increased available N and P in the field, increased germination of *Paspalum* in the field, and facilitated higher biomass and height growth for both *Phytolacca* and *Paspalum* in the screen-house experiment. Forest soils also positively affected soil conditions and facilitated seedling biomass and height growth, but not to the degree of fertilizer. Despite the nutrients associated with the foliar material of *Cecropia* and *Cyathea* litter, these two soil additions had little positive effect on soil fertility and no positive effects on seedling biomass and height growth. *Cecropia* decomposed more slowly and retained more foliar N, and therefore inhibited *Paspalum* germination in the short-term. However, long-term (>1 yr) increases to soils and plants resulting from decomposition and N release from *Cecropia* are possible. Therefore, previous predictions that organic matter in general is necessary for plant colonization may be misleading, as forest soil was the only organic matter treatment that facilitated plant colonization through increasing seedling biomass and height growth on landslides in Puerto Rico.

Soil nutrients are quickly lost from landslide soils (especially in the field), showing that nutrient availability of treatments (especially fertilizer and forest soil) are constrained by time. It is clear from this study that in order to facilitate seedling establishment and growth, it is critical that fertilizer and forest soil treatments be added to landslide soils in concert with seed sowing in order to maximize nutrient uptake by seedlings before the occurrence of substantial treatment loss. Accelerating the establishment of seeds, and the

growth of seedlings, will contribute to soil stability and could accelerate the rate of succession on landslides.

Table 2.1. Site characteristics for the five landslides used for the field experiment in the LEF, Puerto Rico. Light was determined at ground level by averaging three measurements taken between noon and 2 pm local time on a day with <10% cloud cover.

Site	Elevation (m a.s.l.)	Area (m <sup>2</sup> )	Aspect	Slope (°)	Light ( $\mu$ Einsteins m <sup>-2</sup> s <sup>-1</sup> )
ES5	580	2923	NW	14	2267
ES10	600	1440	NE	21	1750
J4	460	1457	NW	23	-
RB10	600	810	E	15	1867
MY8	750	1512	NE	27	-

Table 2.2. Summary table of repeated-measures MANOVA for the three field available soil nitrogen variables:  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , N-mineralization. Measurements were at 45 and 360 d. Sites include the five landslides, and treatments include the five soil treatments. P-values for between subjects are based on F-values, and P-values for within subjects are based on results of Wilks' Lambda values.

Source	Num d.f.	Den. d.f.	P
<b>Between Subjects</b>			
Site	4	43	0.0049
Treatment	4	43	<0.0001
Site*Treatment	16	43	0.0026
<b>Within Subjects</b>			
Variable*Time	3	41	<0.0001
Variable*Time*Site	12	109	0.0072
Variable*Time*Treatment	12	109	<0.0001
Variable*Time*Site*Treatment	48	123	0.0606

Table 2.3. Summary table for the between-subject comparisons (averaged across time) P-values for each of the variable in the full model repeated-measures MANOVA shown in Table 2.2. The three soil variables from the available N field experiment are:  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , N-mineralization. Sites include the five landslides, and treatments include the five soil treatments.

Source	df	$\text{NH}_4^+$	$\text{NO}_3^-$	N-mineralization
Site	4	0.0332	0.3491	0.0284
Treatment	4	0.3694	<0.0001	0.0004
Site x Treatment	16	0.8127	0.8496	0.0010

Table 2.4. Soil  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations ( $\mu\text{g g soil}^{-1}$ ) 45 and 360 d following soil treatments (mean $\pm$ SE). Treatment means are from five landslides in the LEF, Puerto Rico. Different letters within columns during the 45 d sampling indicate significant differences between treatments.

Treatment	$\text{NH}_4^+$	$\text{NO}_3^-$	$\text{NH}_4^+$	$\text{NO}_3^-$
	45 d		360 d	
<i>Cecropia</i>	0.03 $\pm$ 0.01 <sup>a</sup>	1.02 $\pm$ 0.33 <sup>a</sup>	7.62 $\pm$ 4.09	2.28 $\pm$ 0.53
<i>Cyathea</i>	0.07 $\pm$ 0.04 <sup>a</sup>	1.77 $\pm$ 0.45 <sup>a</sup>	3.37 $\pm$ 0.59	2.85 $\pm$ 1.00
Forest soil	0.19 $\pm$ 0.07 <sup>a</sup>	4.29 $\pm$ 1.18 <sup>a</sup>	3.90 $\pm$ 0.59	2.22 $\pm$ 0.83
Fertilizer	0.89 $\pm$ 0.31 <sup>b</sup>	26.06 $\pm$ 5.24 <sup>b</sup>	3.62 $\pm$ 0.55	3.15 $\pm$ 0.92
Control	0.12 $\pm$ 0.05 <sup>a</sup>	2.04 $\pm$ 0.68 <sup>a</sup>	2.95 $\pm$ 0.32	3.31 $\pm$ 1.07

Table 2.5. Summary table of repeated-measures MANOVA for the six field soil variables: SOM, total N, available P, total P, moisture, and pH. The soil variables (subtracted from pre-treatment values) were measured at 60, 210, and 370 d. Sites include the five landslides, and treatments include the five soil treatments. P-values for between subjects are based on F-values, and P-values for within subjects are based on results of Wilks' Lambda values.

Source	Num. d.f.	Den. d.f.	P
<b>Between Subjects</b>			
Site	4	50	0.1910
Treatment	4	50	0.3294
Site x Treatment	16	50	0.8302
<b>Within Subjects</b>			
Variable*Time	12	39	<0.0001
Variable*Time*Site	48	152	<0.0001
Variable*Time*Treatment	48	157	0.0168
Variable*Time*Site*Treatment	192	402	0.6616

Table 2.6. Summary table for the between-subject comparisons (averaged across time) P-values for each of the variable in the full model repeated-measures MANOVA shown in Table 2.5. The six soil variables from the field experiment are: SOM, total N, available P, total P, pH, and moisture. Sites include the five landslides, and treatments include the five soil treatments.

Source	df	Total N	Total P	Avail P	Moist	SOM	pH
Site	4	0.0002	0.7770	0.3615	<0.0001	0.0007	0.0045
Treatment	4	0.0569	0.3227	0.4364	0.7748	0.0233	<0.0001
Site x Treatment	16	0.9767	0.7377	0.8113	0.9527	0.6011	0.7368



Table 2.7. Summary table of repeated-measures MANOVA for the *Cecropia* and *Cyathea* litterbag decomposition experiment measured at 60, 150, 300, and 365 d. Sites include the five landslides, and treatments include the two litter types. P-values for the between subjects are based on F-values, and P-values for the within subjects are based on results of Wilks' Lambda values.

Source	Num. d.f.	Den. d.f.	P
<b>Between Subjects</b>			
Site	4	20	0.0045
Treatment	1	20	<0.0001
Site*Treatment	4	20	0.1246
<b>Within Subjects</b>			
Time	3	18	<0.0001
Time*Site	12	48	0.0015
Time*Treatment	3	18	0.0146
Time*Site*Treatment	12	48	0.0208

Table 2.8. Total foliar nitrogen and total foliar phosphorus concentrations ( $\text{mg g}^{-1}$ ) for *Cecropia* and *Cyathea* used in a decomposition study on five landslides in the LEF, Puerto Rico (mean $\pm$ SE).  $T_0$  represents dead foliar material analyzed before litterbag addition, and  $T_1$  represents concentrations after one year of litterbag decomposition on landslides. Significant differences, determined by t-tests for  $T_0$  and a two-way ANOVA for  $T_1$ , are indicated by differing letters within each column.

Species	Total N $T_0$	Total N $T_1$	Total P $T_0$	Total P $T_1$
<i>Cecropia</i>	$9.24 \pm 0.09^a$	$10.12 \pm 0.95^a$	$0.21 \pm 0.03^a$	$0.12 \pm 0.02^a$
<i>Cyathea</i>	$8.18 \pm 0.31^b$	$3.87 \pm 0.32^b$	$0.21 \pm 0.01^a$	$0.12 \pm 0.03^a$

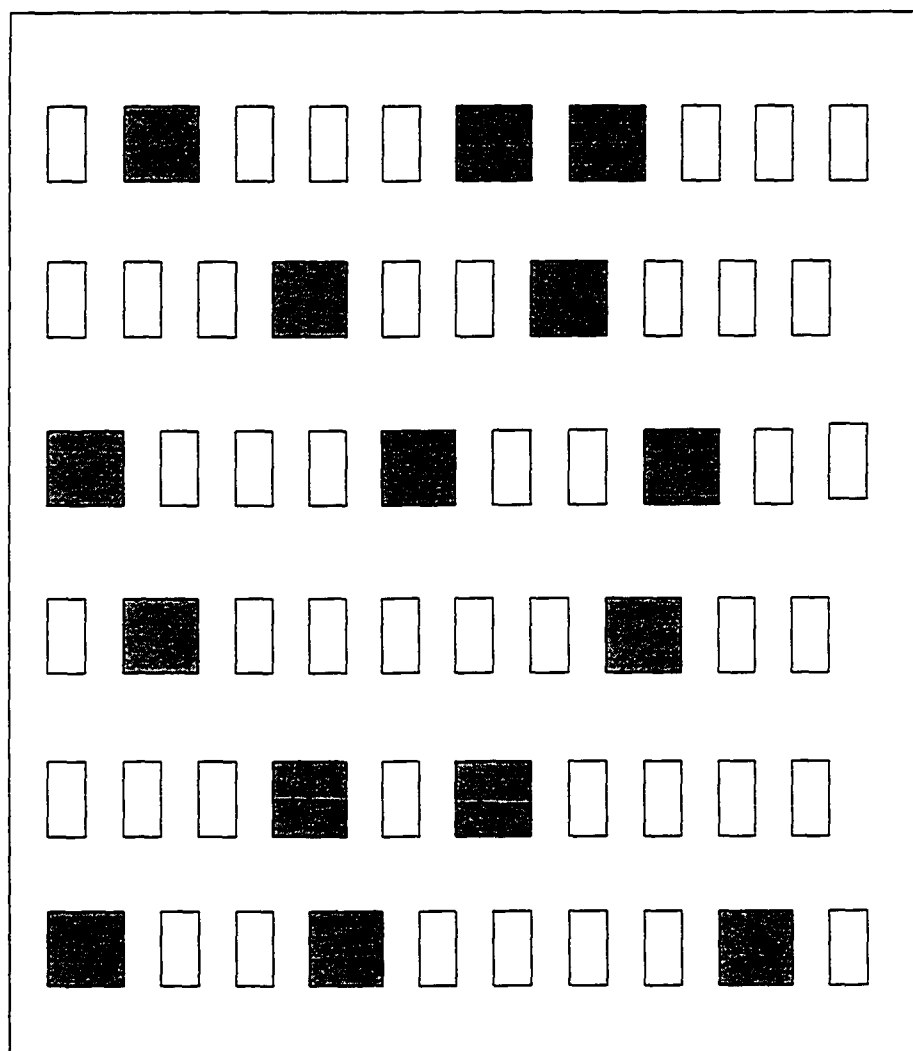
Table 2.9. Summary table of repeated-measures MANOVA for *Paspalum* height and biomass variables for the 80, 160, and 245 d time periods for the screen-house experiment. Treatments include the five soil treatments: *Cecropia*, *Cyathea*, forest soil, fertilizer, and control. P-values for the within subjects are based on Wilks' Lambda values, and P-values for between subjects are based on F-values.

Source	Num. d.f.	Den. d.f.	Complete Model	Seedling Height	Seedling Biomass
<b>Between Subjects</b>					
Treatment	4	35	<0.0001	<0.0001	<0.0001
<b>Within Subjects</b>					
Variable*Time	4	32	<0.0001		
Variable*Time*Treatment	16	98	<0.0001		

Table 2.10. Summary table of repeated-measures MANOVA for *Phytolacca* height and biomass variables for the 80 and 160 d time periods for the screen-house experiment. Treatments include the five soil treatments: *Cecropia*, *Cyathea*, forest soil, fertilizer, and control. P-values for the within subjects are based on Wilks' Lambda values, and P values for between subjects are based on F-values.

Source	Num. d.f.	Den. d.f.	Complete Model	Seedling Height	Seedling Biomass
<b>Between Subjects</b>					
Treatment	4	35	<0.0001	<0.0001	<0.0001
<b>Within Subjects</b>					
Variable*Time	2	34	0.0002		
Variable*Time*Treatment	8	68	<0.0001		

Figure 2.1. Schematic of field soil treatment trays spread across a bare portion of a landslide. Each small (10 x 20 cm) and large (20 x 20 cm) box had one of the five soil treatments (i.e., *Cecropia*, *Cyathea*, forest soil, fertilizer, control) mixed to 10 cm depth, and the small seeded boxes also had one of the three seed treatments (i.e., *Phytolacca*, *Paspallum*, unseeded control) added to the soil surface. The arrow represents the direction of the landslide slope.



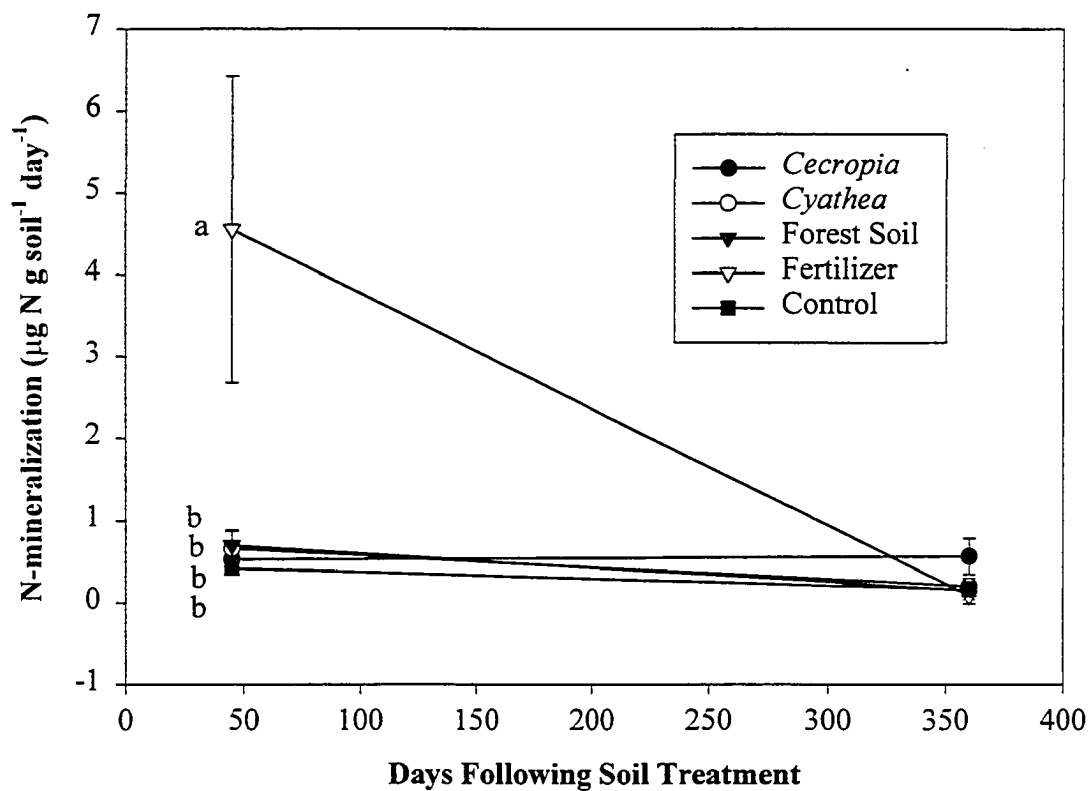


Figure 2.2. Mean ( $\pm$ SE) soil nitrogen mineralization per day, measured 45 d and 360 d following soil treatments on five landslides used in the field experiment in the LEF, Puerto Rico. Soils were incubated *in situ* for 14 d. Different letters indicate significant treatment differences for the 45 d sampling period.

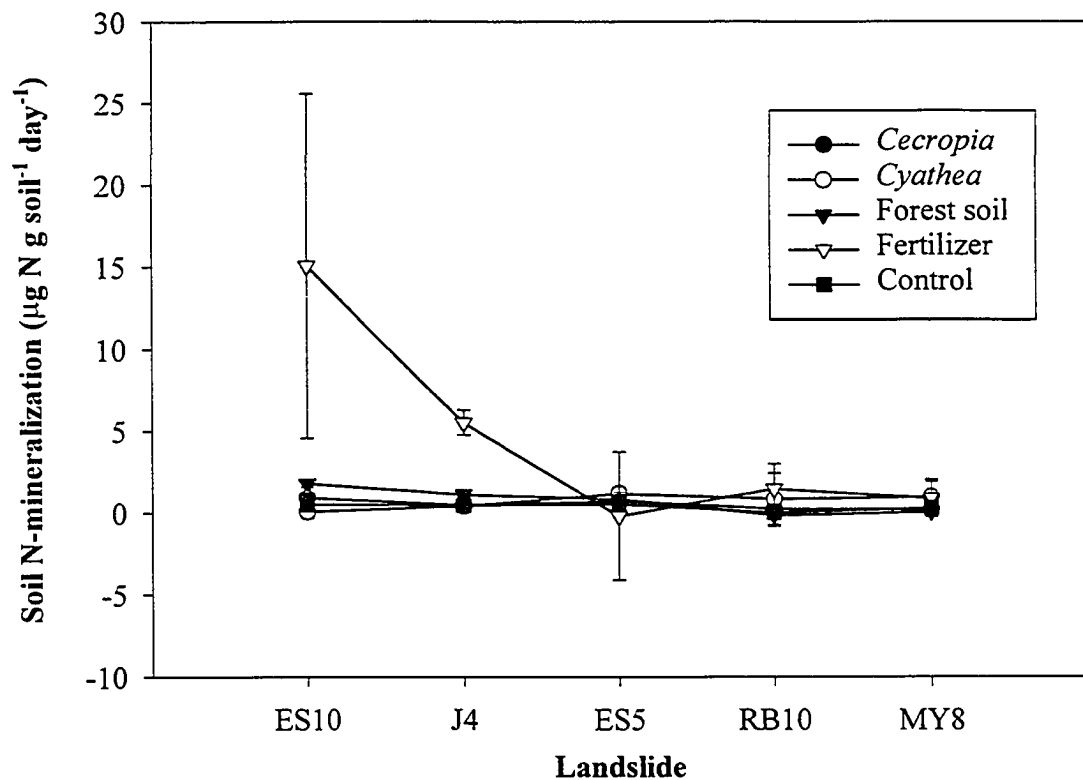


Figure 2.3. Mean ( $\pm$ SE) N-mineralization concentrations 45 d following treatment addition on five landslides in the LEF, Puerto Rico. Soils were incubated for 14 d *in situ*. Crossing lines between landslides support significant site x treatment interaction determined in analysis ( $P=0.0003$ ).

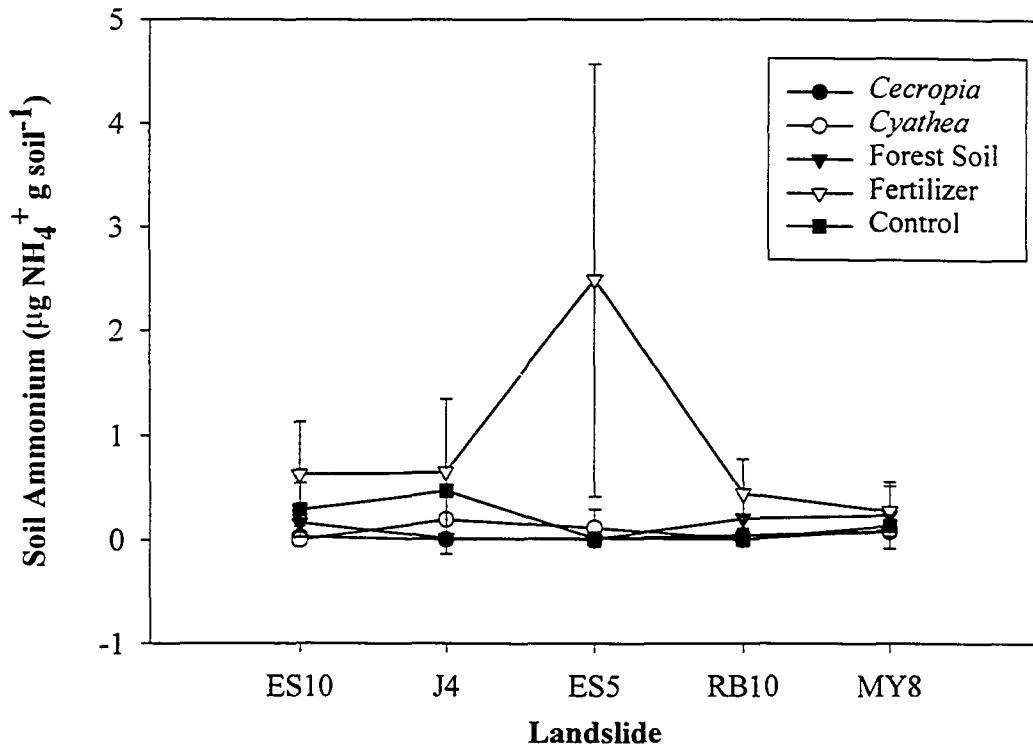


Figure 2.4. Mean ( $\pm$ SE) soil ammonium concentrations 45 d following treatment additions. Treatment means are shown for each landslide. Crossing lines between landslides support significant site x treatment interaction determined in analysis ( $P=0.03$ ).



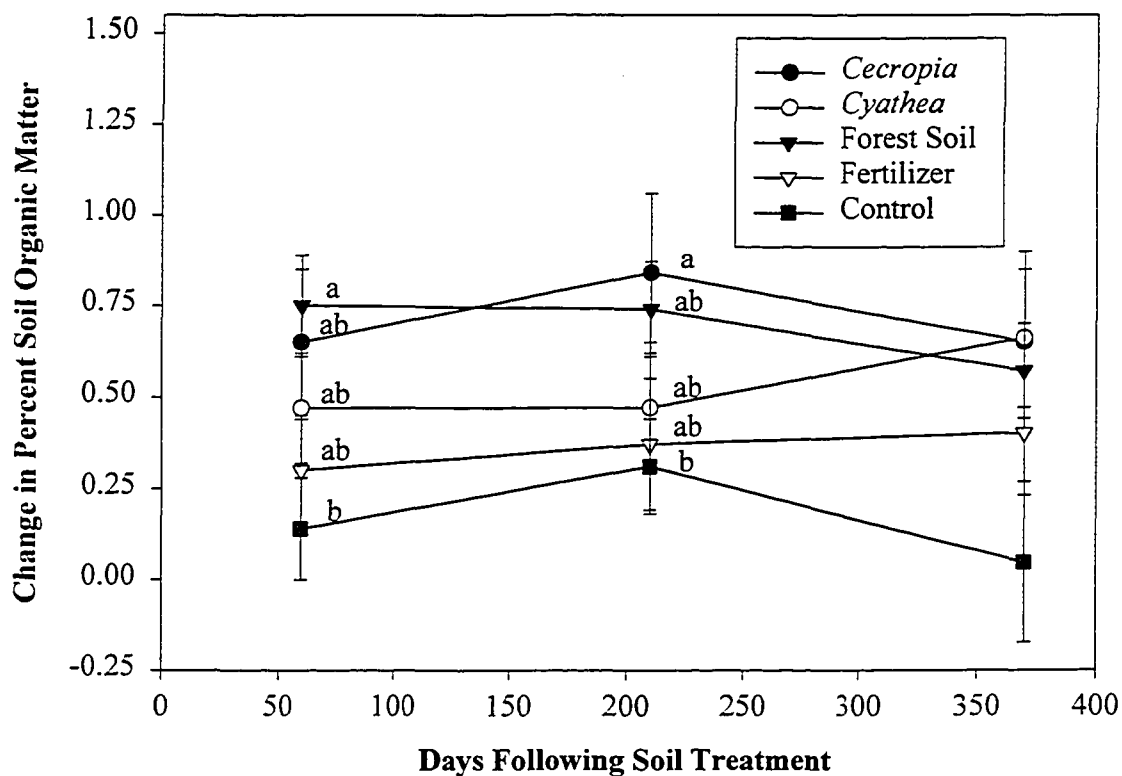


Figure 2.5. Mean ( $\pm$ SE) percent change in soil organic matter (SOM) for five soil treatments averaged over five landslides in the LEF, Puerto Rico. Means for each sampling period (60, 210, and 370 d) were differences from pre-treatment SOM. Different letters indicate significant treatment differences within a given sampling period.

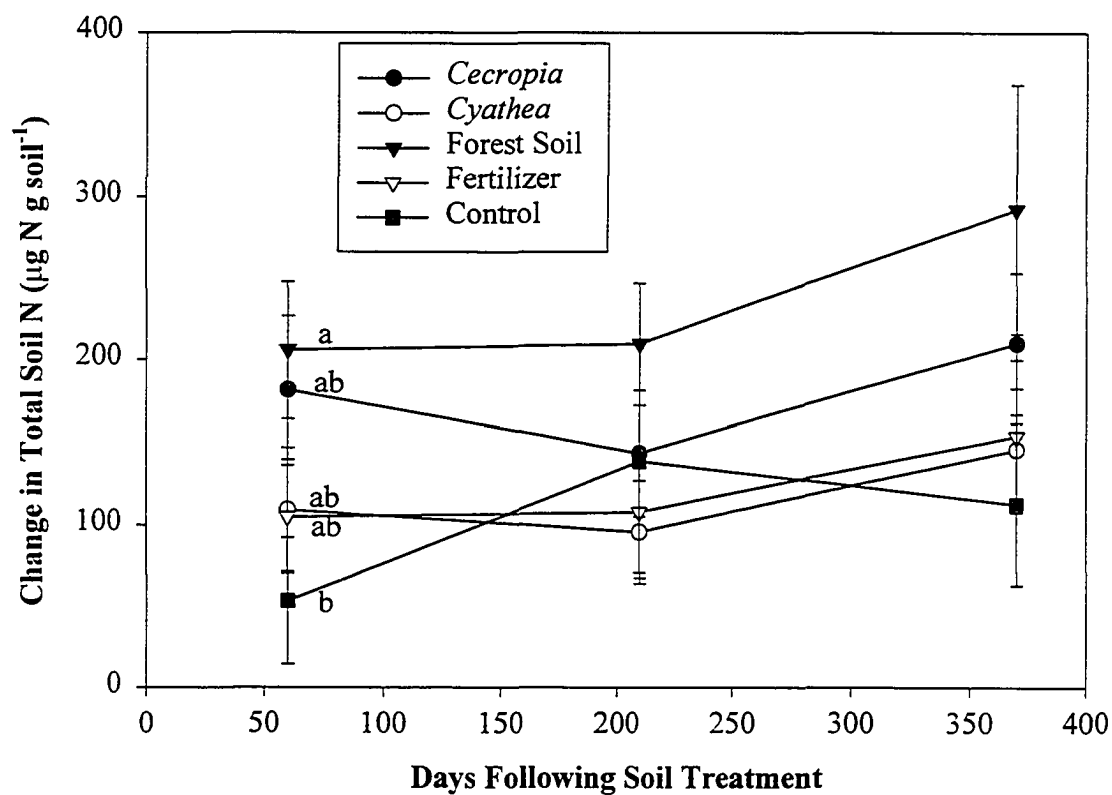


Figure 2.6. Mean ( $\pm$ SE) change in total soil nitrogen for five soil treatments summed over five landslides in the LEF, Puerto Rico. Means for each sampling period (60, 210, and 370 d) were differences from pre-treatment soil total nitrogen concentrations. Different letters indicate significant treatment differences for the 60 d sampling period.

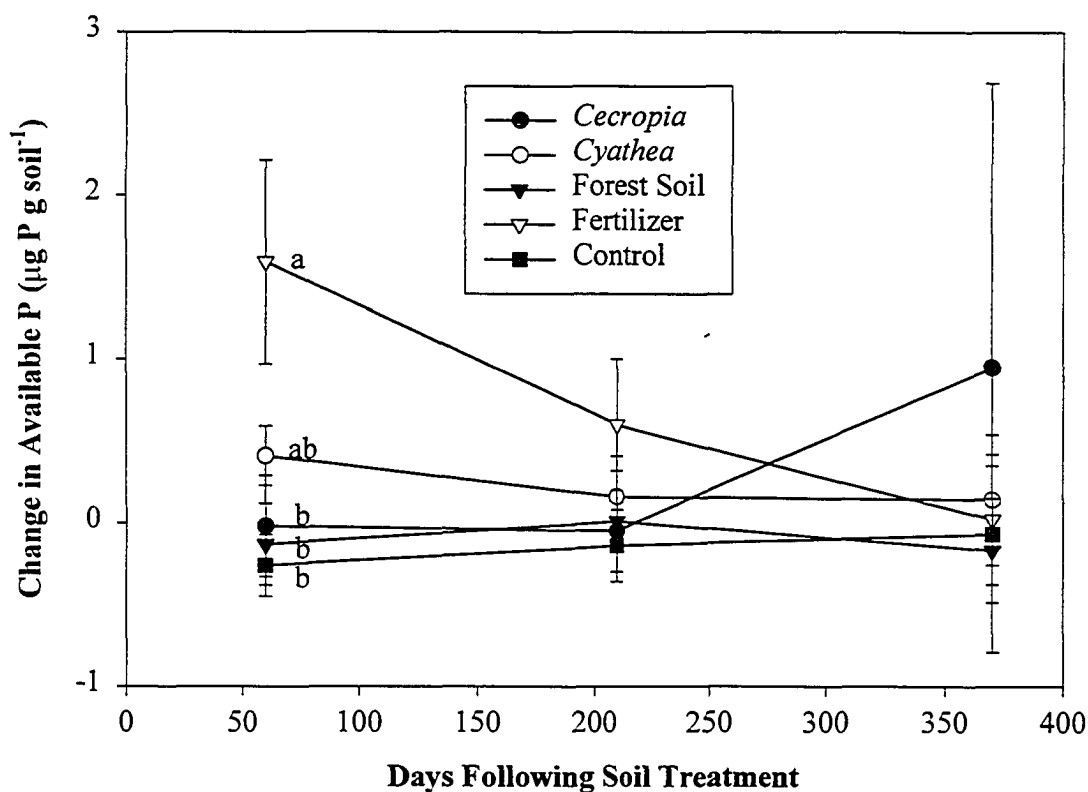


Figure 2.7. Mean ( $\pm$ SE) change in available soil phosphorus for five soil treatments averaged over five landslides in the LEF, Puerto Rico. Means for each sampling period (60, 210, and 370 d) were differences from pre-treatment soil available phosphorus concentrations. Different letters indicate significant treatment differences for the 60 d sampling period.

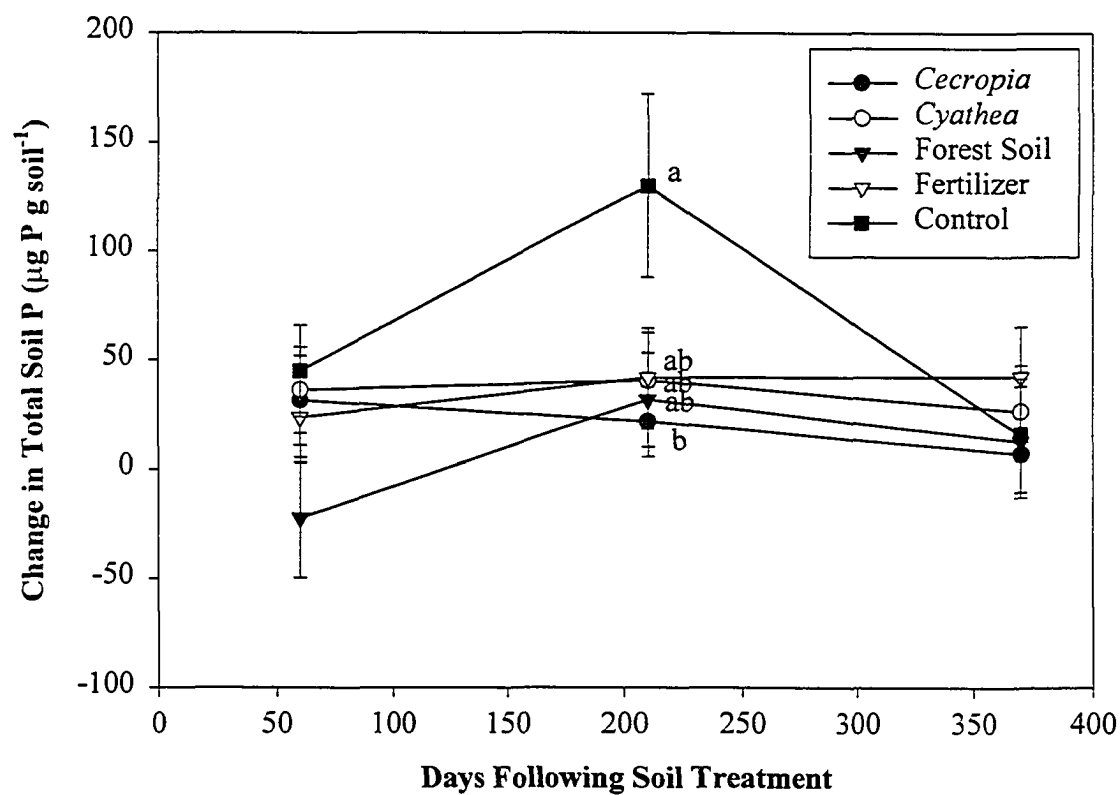


Figure 2.8. Mean ( $\pm$ SE) change in total soil phosphorus for five soil treatments averaged over five landslides in the LEF, Puerto Rico. Means for each sampling period (60, 210, and 370 d) were differences from pre-treatment soil total phosphorus concentrations. Different letters indicate significant treatment differences within a sampling period.

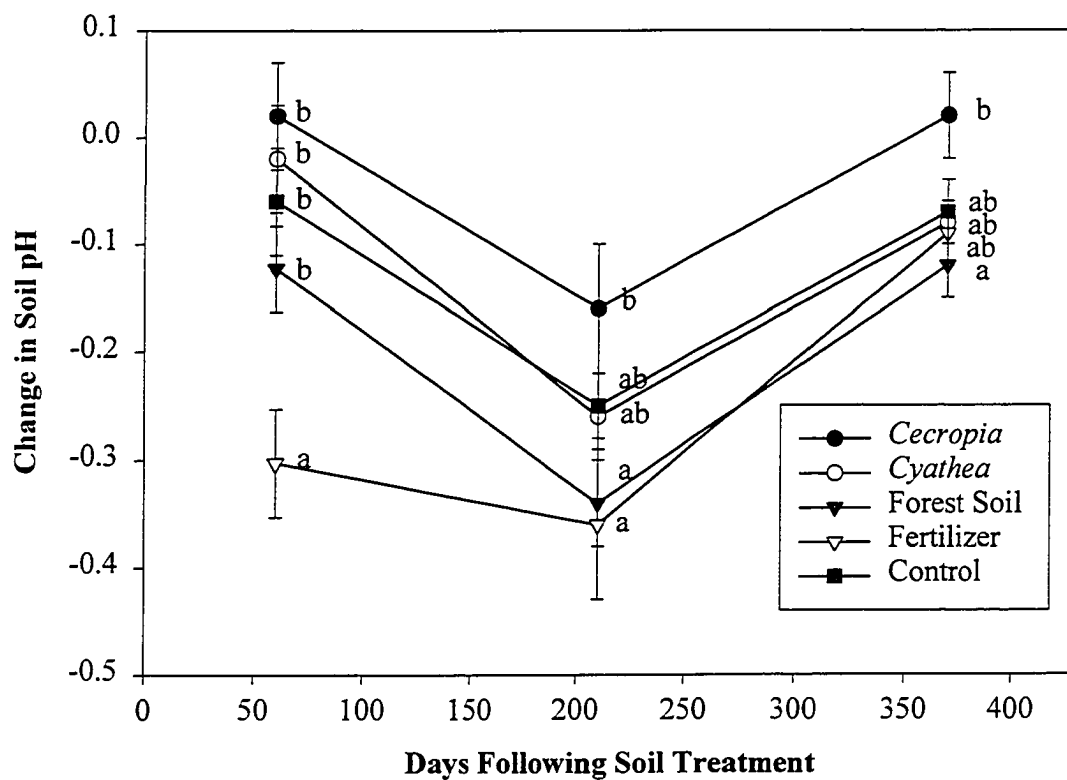


Figure 2.9. Mean ( $\pm$ SE) percent change in soil pH for five soil treatments averaged over five landslides in the LEF, Puerto Rico. Means for each sampling period (60, 210, and 370 d) were differences from pre-treatment pH. Different letters indicate significant treatment differences for respective sampling periods.

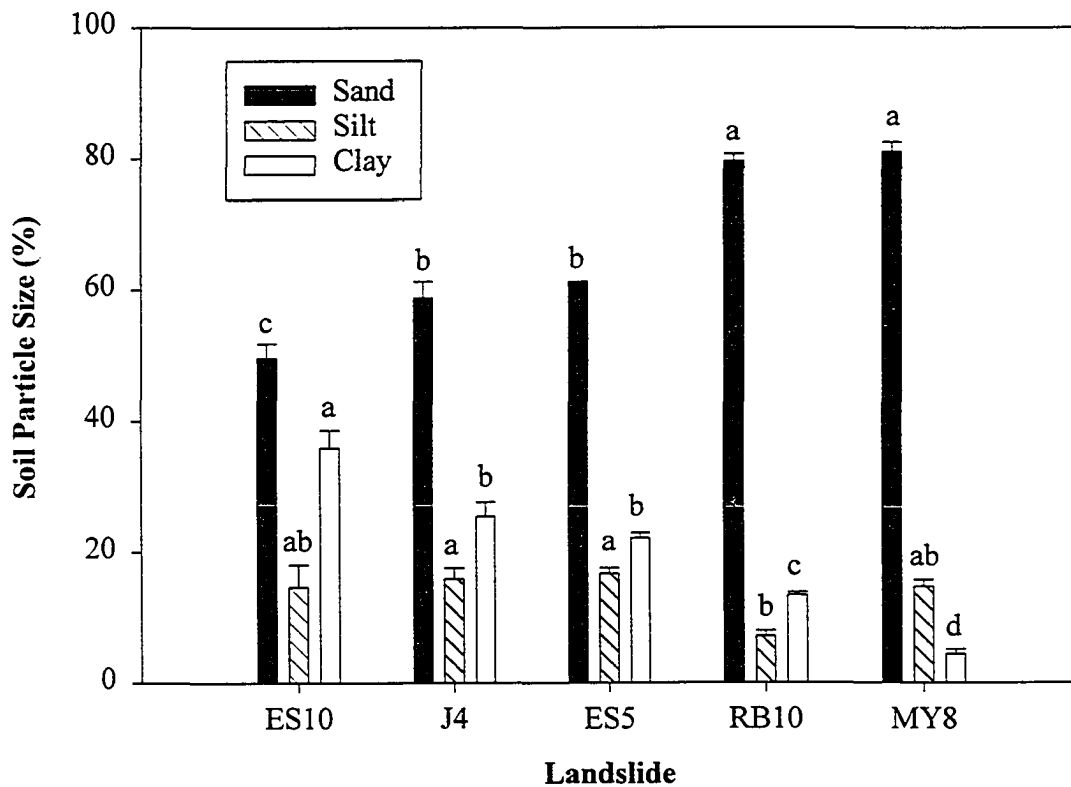


Figure 2.10. Mean ( $\pm$ SE) sand, silt, and clay particle size fractions taken from each landslide in the LEF, Puerto Rico. Soils were sampled from unaltered areas in the five landslides used in the soil treatment addition experiment. Different letters indicate significant landslide differences among similar particle size fractions.

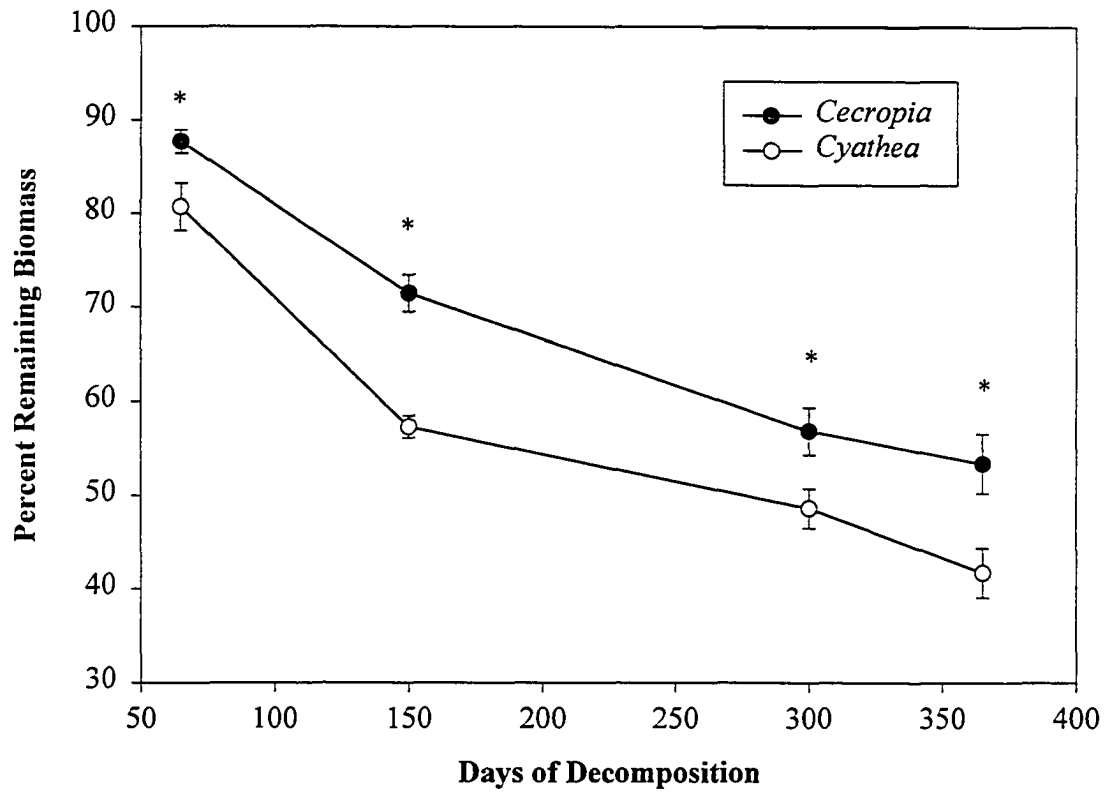


Figure 2.11. Mean ( $\pm$ SE) percent biomass remaining of *Cecropia* and *Cyathea* foliar material on five landslides in the LEF, Puerto Rico. Significant differences between species decomposition for each collections period (60, 150, 300, and 365 d) are indicated by an asterix (\*).

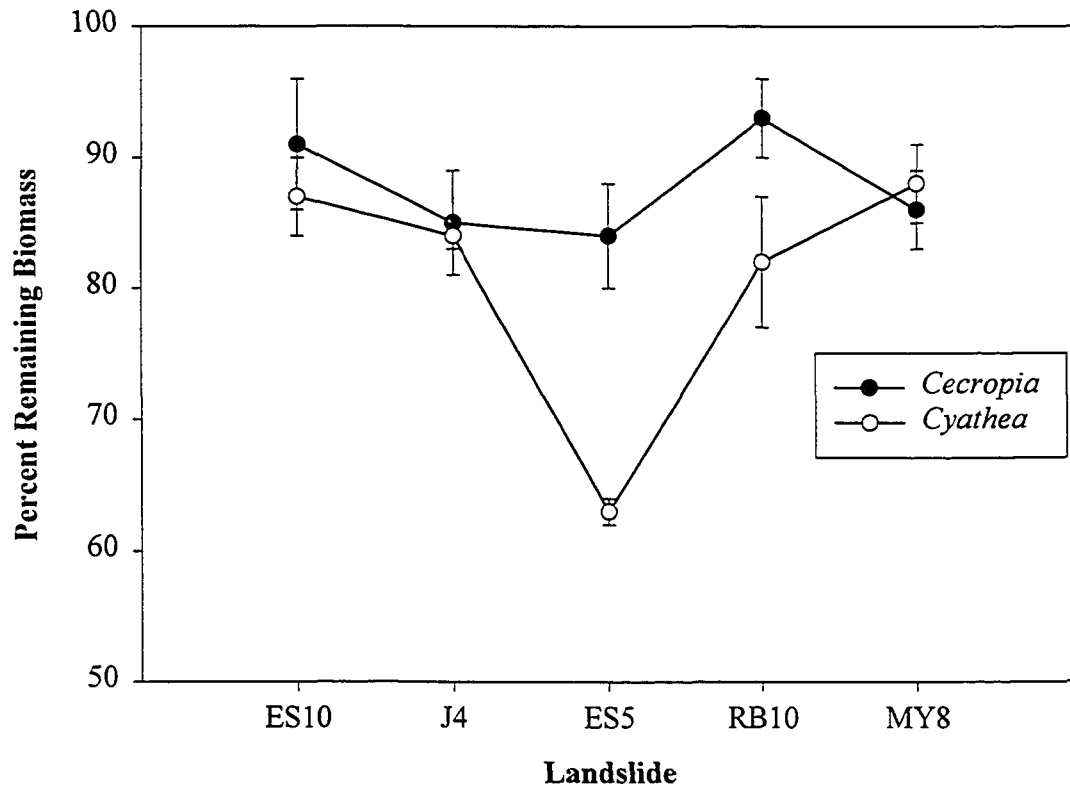


Figure 2.12. Mean ( $\pm$ SE) percent biomass of *Cecropia* and *Cyathea* foliar material 60 d after on-set of experiment on five landslides in the LEF, Puerto Rico. Landslide MY8 supports the site  $\times$  treatment interaction determined in analysis ( $P < 0.0001$ ).



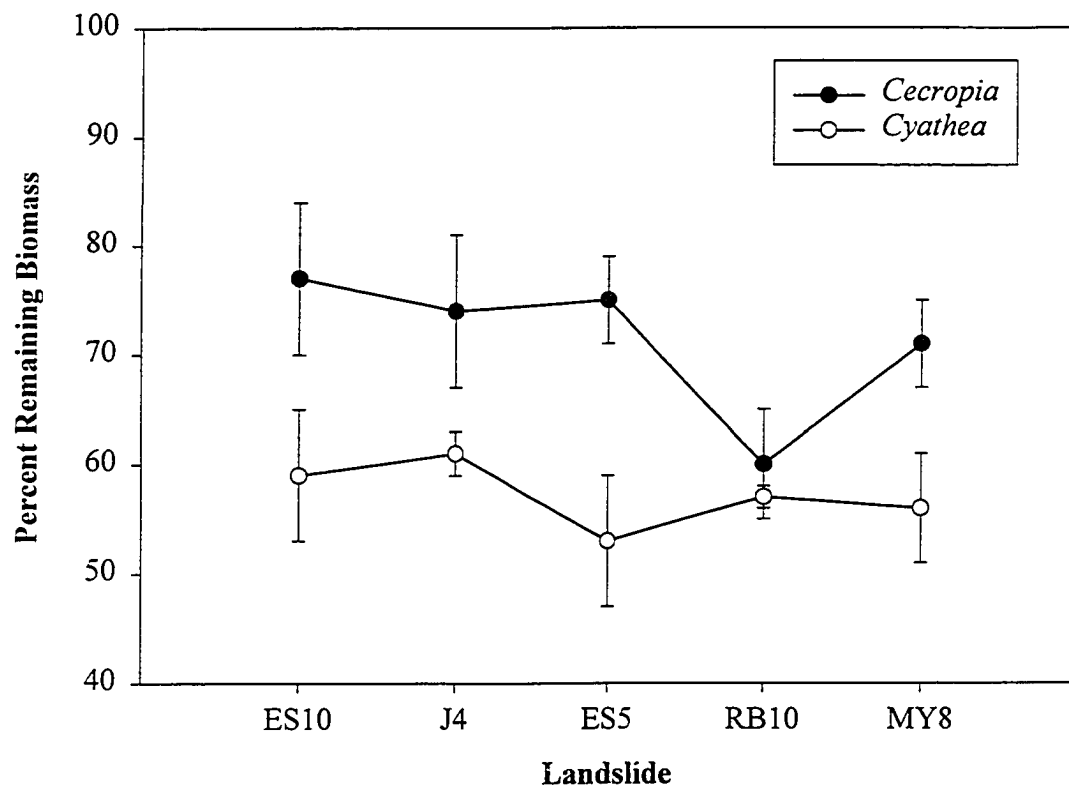


Figure 2.13. Mean ( $\pm$ SE) percent biomass remaining of *Cecropia* and *Cyathea* foliar material 150 d after on-set of experiment in the LEF, Puerto Rico. Landslide RB10 supports the site x treatment interaction determined in analysis ( $P=0.04$ ).

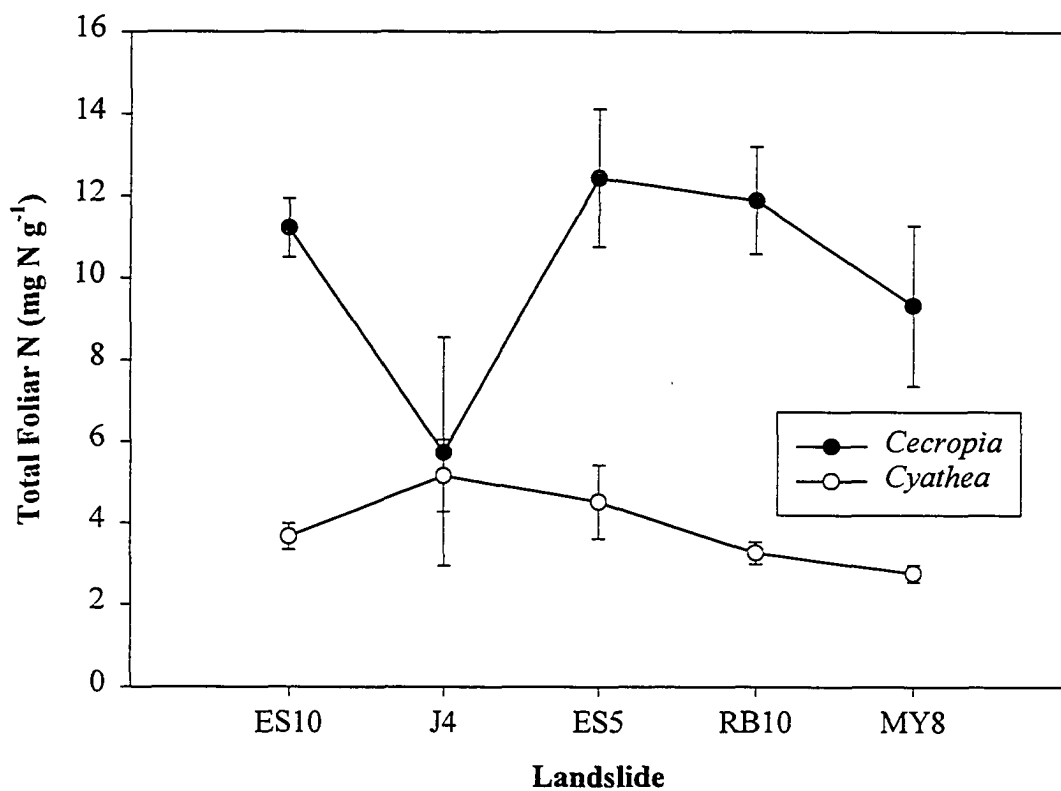


Figure 2.14. Mean ( $\pm$ SE) total foliar nitrogen concentrations of *Cecropia* and *Cyathea* litter after one year of decomposition on five landslides in the LEF, Puerto Rico. Landslide J4 supports the site x treatment interaction determined in analysis ( $P=0.05$ ).

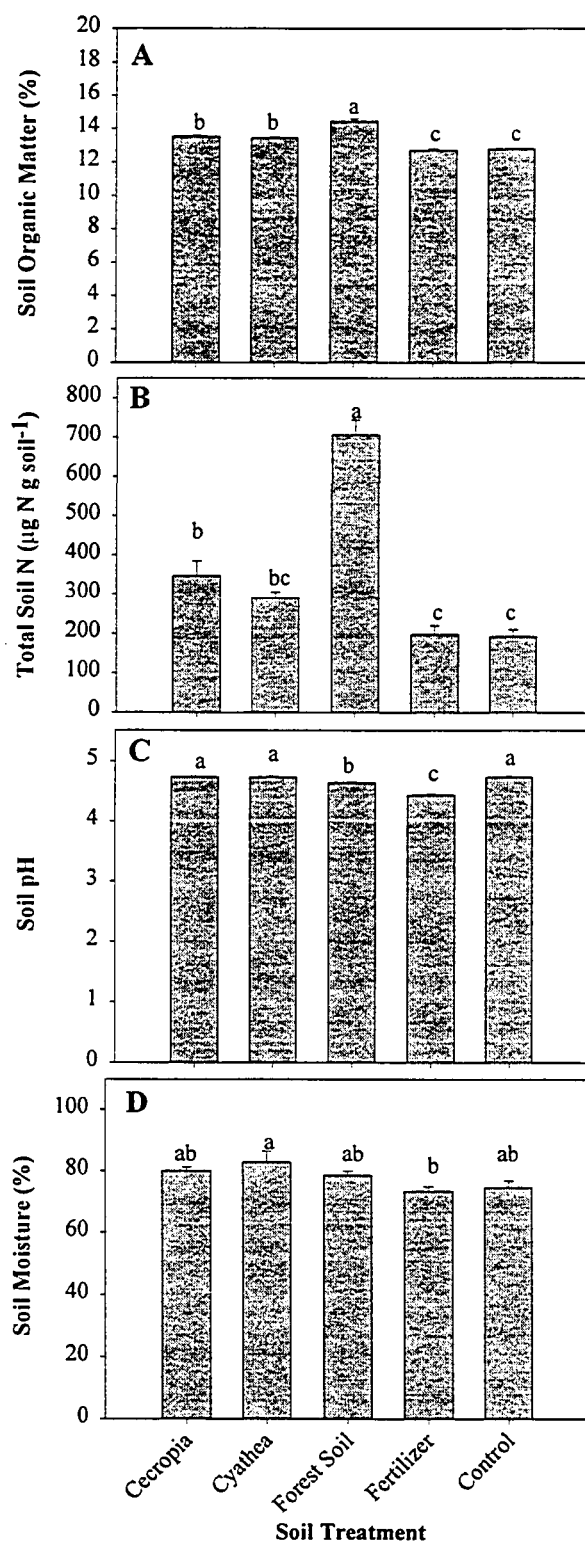


Figure 2.15. Mean ( $\pm$  SE) for respective soil variables sampled in the screen-house experiment at EVFS, Puerto Rico. Sampling took place one year following soil treatment additions to landslide soil. Different letters indicate significant treatment differences.

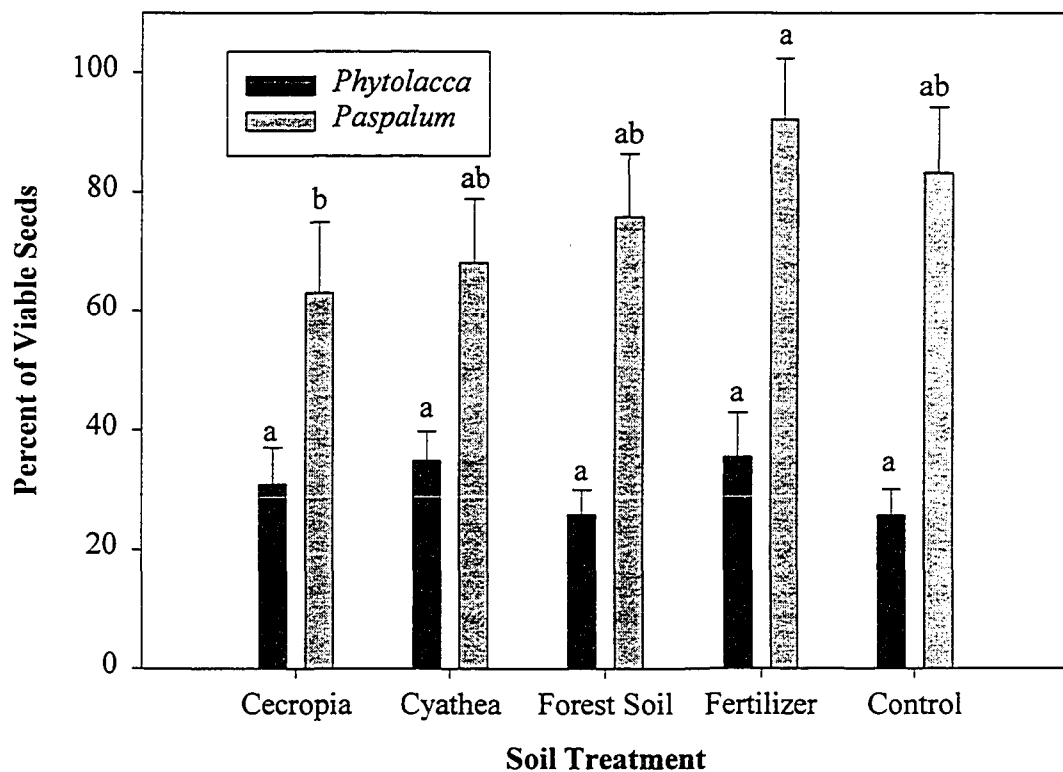


Figure 2.16. Mean ( $\pm$ SE) percent seed germination (% of viable seeds) of *Phytolacca* and *Paspalum* sown in the five soil treatments on five landslides in the LEF, Puerto Rico. Different letters for respective seed types indicate significant differences among soil treatments.

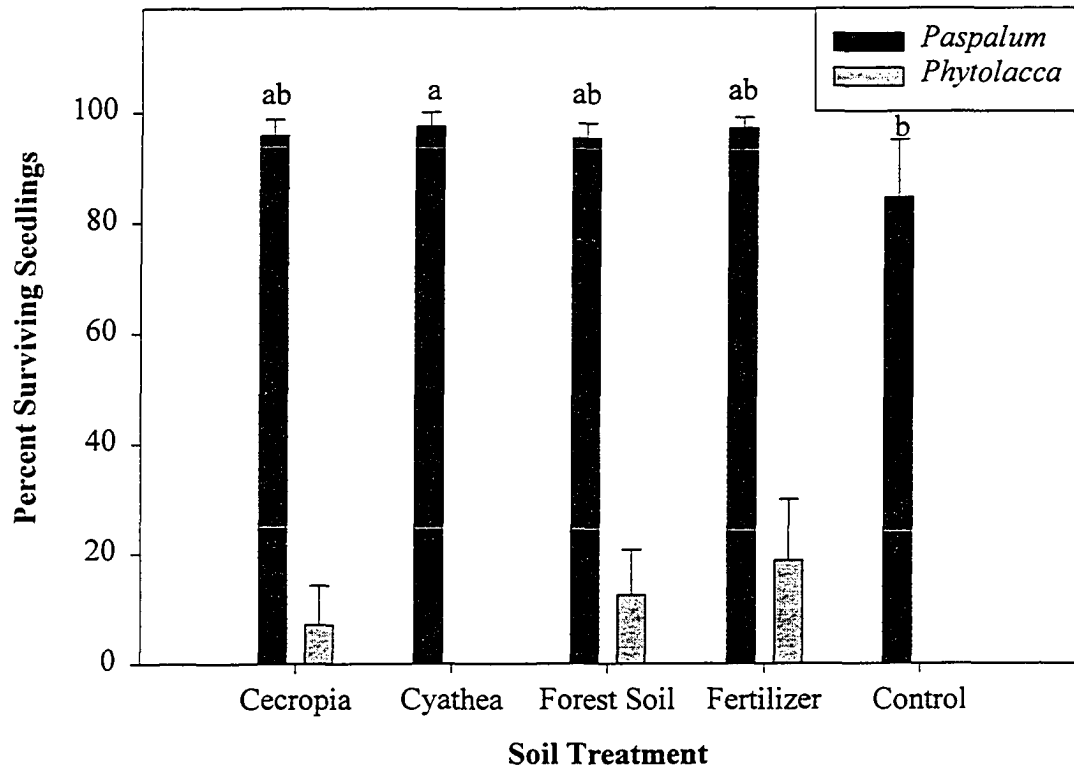


Figure 2.17. Mean ( $\pm$ SE) percent surviving seedlings for five soil treatments used in the field seedling experiment in the LEF, Puerto Rico. Seedling means are from five landslides, one year following soil treatment addition. Survival was based on the number of individuals surviving from 80 d after seed sowing to 235 d after sowing. Different letters for *Paspalum* indicate significant differences among treatments after means were arcsin square-root transformed.

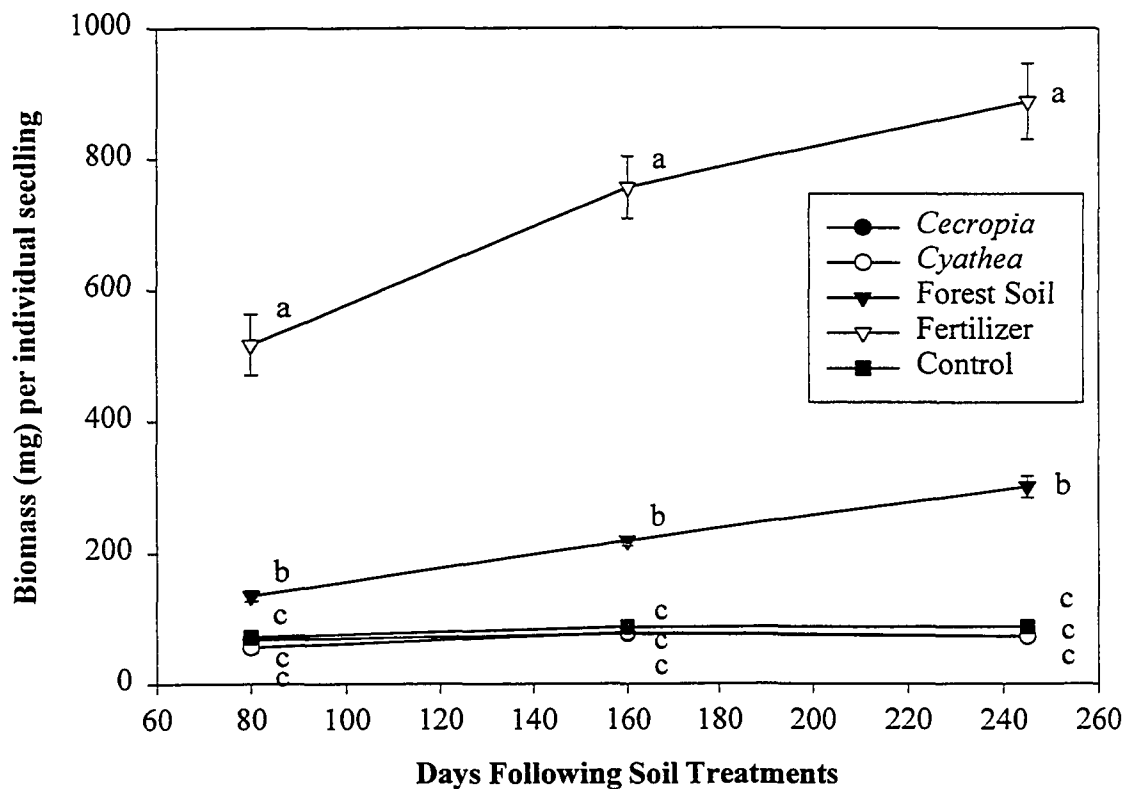


Figure 2.18. Mean ( $\pm$ SE) *Paspalum* biomass (mg indiv.<sup>-1</sup>) measured during 80, 160, and 245 d after soil treatment additions to the screen-house experiment. Different letters during each respective time period indicate significant differences among treatments.

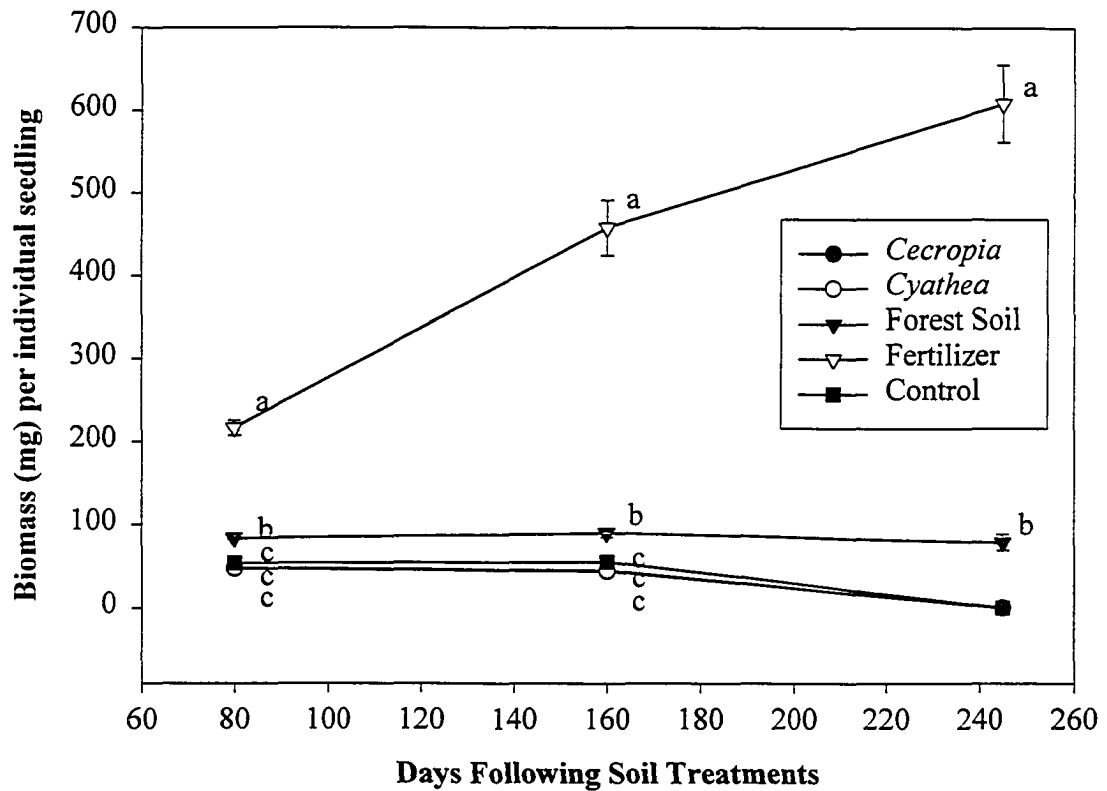


Figure 2.19. Mean ( $\pm$ SE) *Phytolacca* biomass (mg indiv.<sup>-1</sup>) measured during 80, 160, and 245 d after soil treatment additions to the screen-house experiment. Different letters during each respective sampling period indicate significant differences among treatments. Seedlings in *Cecropia*, *Cyathea*, and control treatments were not present during the 245 d sampling. Therefore, analysis was not conducted on these soil treatments.

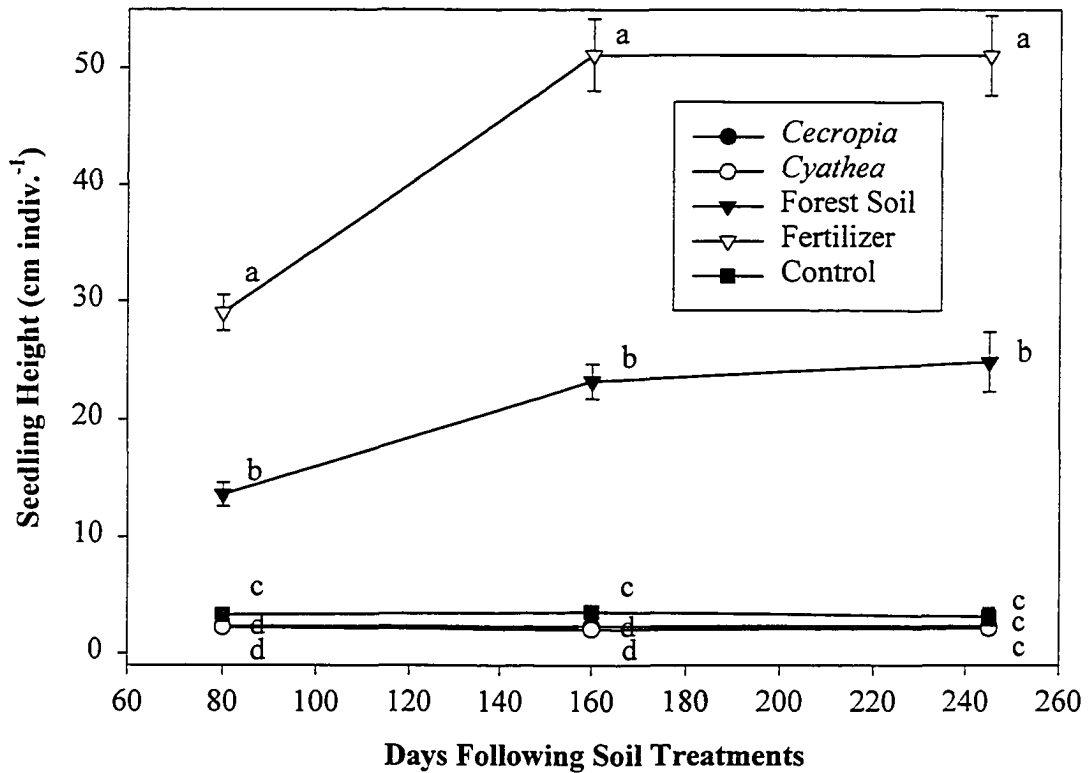


Figure 2.20. Mean ( $\pm$ SE) *Paspalum* seedling heights measured during 80, 160, and 245 d after soil treatment additions to the screen-house experiment. Different letters during each respective time period indicate significant differences among treatments (d signifies *Cecropia* and *Cyathea* for time periods 80 d and 160 d).



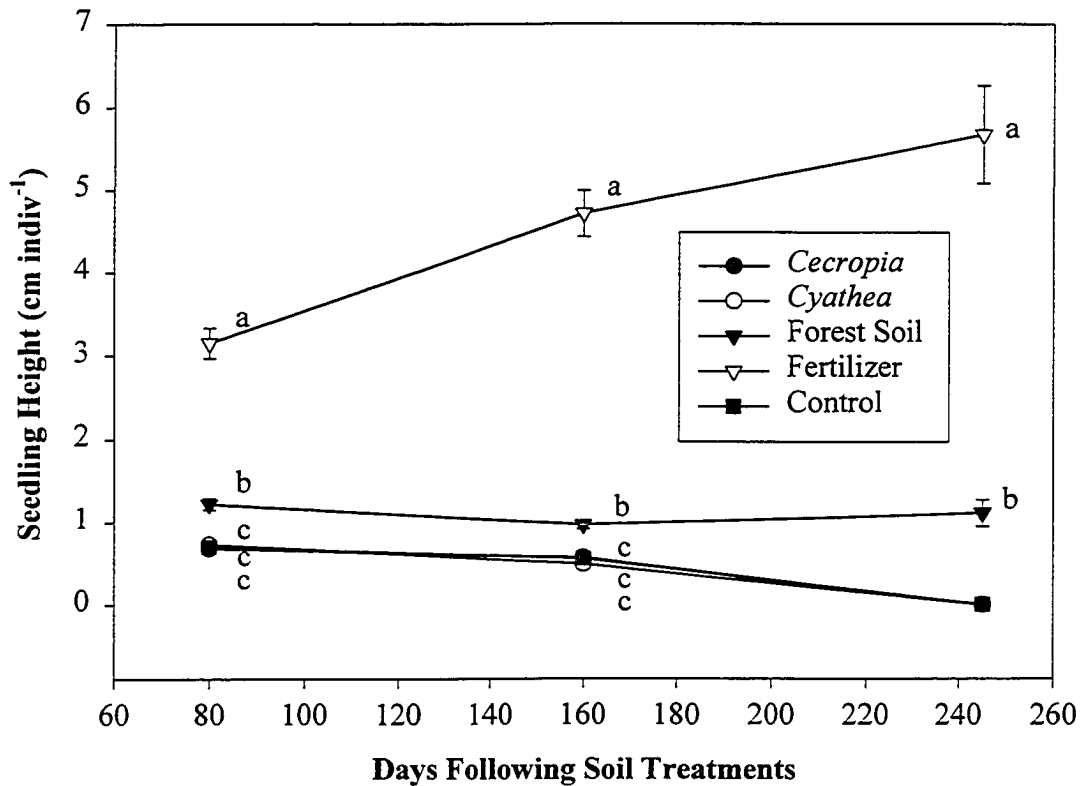


Figure 2.21. Mean ( $\pm$ SE) *Phytolacca* seedling height measured 80, 160, 245 d after soil treatment additions to the screen-house experiment. Different letters during each respective time period indicate significant differences among treatments. Seedlings in *Cecropia*, *Cyathea*, and control treatments were not present during the 245 d sampling. Therefore, analysis was not conducted on these soil treatments.

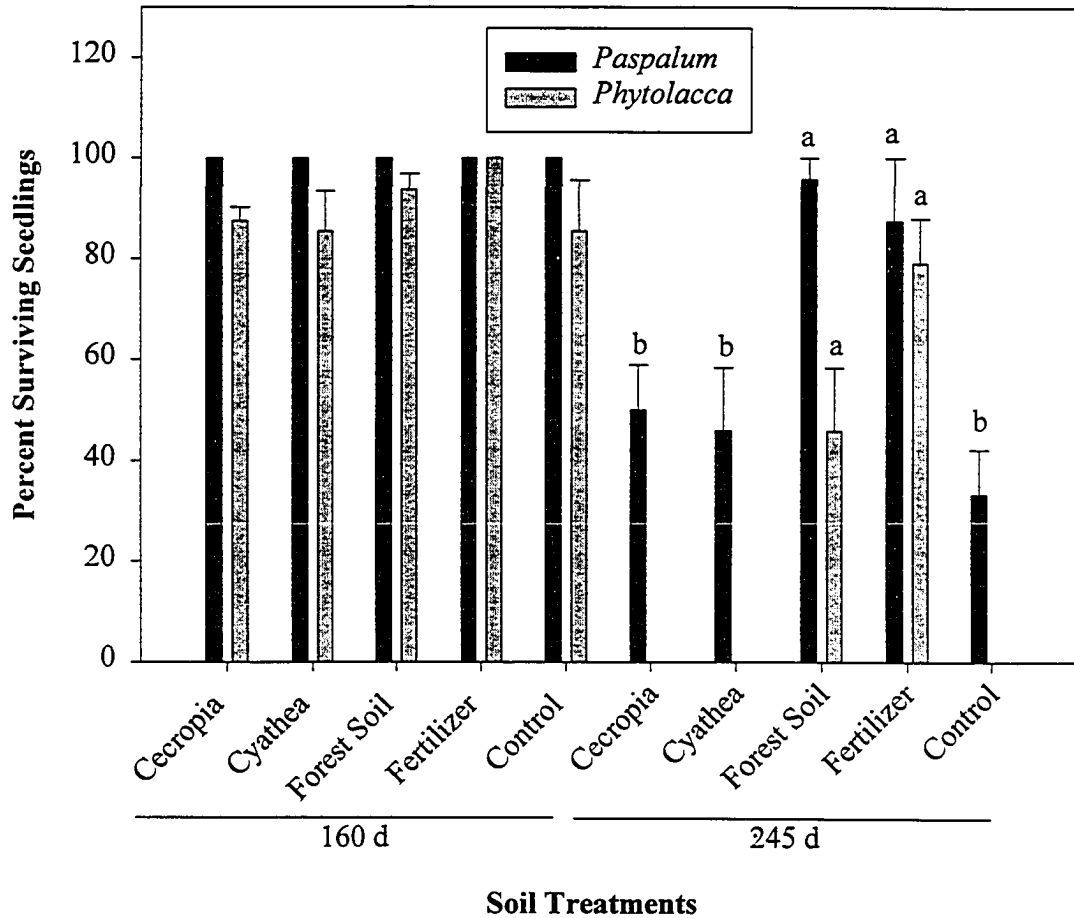
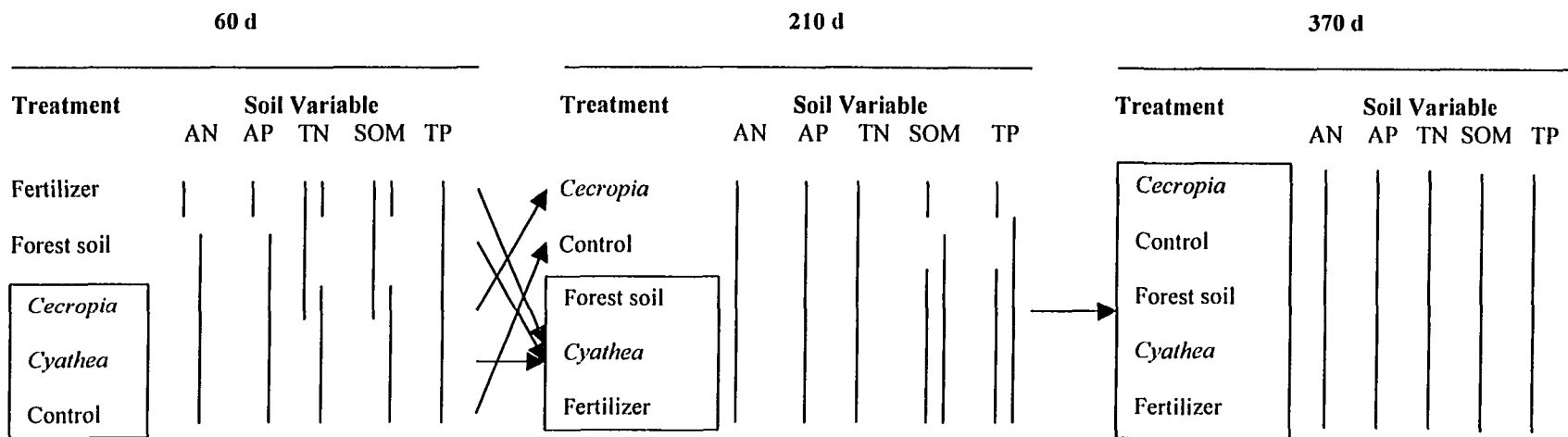


Figure 2.22. Mean ( $\pm$ SE) percent surviving seedlings for five soil treatments used in the screen-house experiment at EVFS, Puerto Rico. The first and second sequence of soil treatments (X-axis) represent survival to 160 and 245 d after soil treatment and seed sowing. Different letters for respective species during the 245 d time period indicate significant differences among treatments. No significant differences were present during the 160 d sampling.

Figure 2.23. Conceptual model ranking the importance (top is most important) of five treatments (additions of commercial fertilizer, forest soil, *Cecropia* leaves, *Cyathea* fronds, and control) used to increase soil nutrients on five landslides in a field experiment in the Luquillo Experimental Forest, Puerto Rico. Rankings were based on the number of significantly different soil variables for each time period. The order used to rank the importance of each soil variables was AN>AP>TN>SOM>TP, where AN=available nitrogen; AP=available P; TN=total nitrogen; SOM=soil organic matter; TP=total phosphorus. For each soil variable, two columns exist to show significant differences between treatments. Vertical lines overlapping treatments indicate no difference. Boxed treatments indicate soil responses that are equal in importance. For example, in the 210 d time period, total P was significantly greater in the control than in *Cecropia*, yet SOM was greater in *Cecropia* than in the control. Because ranking order is SOM>TP, *Cecropia* is ranked higher in importance.



APPENDIX I

FIELD SOILS RAW DATA

APPENDIX Ia. Total soil N and total soil P ( $\mu\text{g N g soil}^{-1}$ ), 0-10 cm depth (mean $\pm$ SE; n=3). T<sub>1</sub>=0 d (time of treatment additions); T<sub>2</sub>=60 d following treatment additions; T<sub>3</sub>=210 d following treatment additions; T<sub>4</sub>=370 d following treatment additions.

Landside	Time	TKN T <sub>1</sub>		TKN T <sub>2</sub>		TKN T <sub>3</sub>		TKN T <sub>4</sub>		TKP T <sub>1</sub>		TKP T <sub>2</sub>		TKP T <sub>3</sub>		TKP T <sub>4</sub>	
		mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
ES10	<i>Cecropia</i>	275.9	74.5	522.5	111.0	534.1	229.3	457.9	106.4	312.7	69.9	270.8	62.4	326.0	79.4	287.7	48.0
	<i>Cyathea</i>	228.5	53.4	442.7	21.8	461.1	35.4	538.2	85.3	294.1	44.3	331.0	54.4	470.9	40.2	389.1	35.1
	For. Soil	253.4	13.5	578.9	104.0	626.4	88.2	689.2	141.2	452.9	123.8	359.6	15.0	496.6	21.3	437.5	21.8
	Control	277.5	97.9	483.1	225.8	535.1	190.5	593.1	269.6	470.0	79.6	425.6	83.1	571.1	111.0	529.6	22.5
J4	Control	353.0	122.7	396.0	40.7	694.2	250.1	513.4	127.1	384.3	84.8	393.1	85.4	629.1	156.8	453.4	77.2
	<i>Cecropia</i>	210.4	76.8	558.0	243.8	374.1	36.3	650.4	90.3	159.4	15.2	130.5	22.6	176.2	14.3	146.0	8.6
	<i>Cyathea</i>	215.5	35.0	314.0	70.5	320.6	58.0	342.6	41.5	222.6	24.4	222.4	22.0	200.9	30.6	224.8	31.0
	Control	145.0	41.4	395.8	122.7	376.2	68.9	734.6	286.4	171.6	23.8	165.5	58.5	229.2	51.4	218.4	27.94
ESS	For. Soil	123.6	47.3	230.4	43.6	290.7	91.9	388.0	78.9	166.4	24.0	227.6	22.1	234.7	38.4	230.7	47.5
	Fertilizer	112.6	45.8	203.8	85.5	236.2	50.3	291.2	107.8	197.8	13.2	213.2	70.0	287.0	70.2	191.6	36.4
	Control	89.4	55.5	159.0	35.4	175.1	10.2	348.3	45.5	392.3	9.4	449.4	31.5	351.5	53.3	343.0	35.2
	Control	147.2	74.5	179.8	25.2	143.4	33.2	244.3	48.8	381.0	5.2	532.1	17.3	398.5	30.3	281.3	12.6
RB10	<i>Cecropia</i>	145.9	48.4	237.0	47.2	177.1	29.1	347.3	20.1	352.2	50.4	365.8	21.8	364.7	51.6	268.5	69.3
	<i>Cyathea</i>	114.6	77.5	189.3	17.3	129.6	22.9	172.4	56.5	346.2	66.4	453.1	55.6	338.2	34.6	334.1	47.4
	For. Soil	119.7	99.0	188.1	10.0	187.8	31.4	262.2	102.1	276.3	49.4	413.8	68.3	349.1	36.5	221.6	32.3
	Control	226.1	32.8	399.5	54.7	304.2	84.1	353.2	110.5	102.2	13.0	171.0	28.4	181.3	36.6	175.1	20.7
MY8	<i>Cecropia</i>	144.6	23.4	363.1	79.4	270.0	46.6	342.8	54.2	172.1	29.2	158.5	17.7	159.3	26.9	223.3	51.1
	<i>Cyathea</i>	133.4	25.3	454.6	72.9	358.4	40.0	314.9	15.1	157.7	14.0	166.4	12.8	159.7	4.3	250.8	23.3
	For. Soil	151.1	35.2	324.6	52.8	255.5	5.9	261.9	37.6	114.9	41.7	125.5	15.4	157.9	6.8	188.3	42.4
	Control	207.9	16.8	292.6	73.0	261.0	21.8	295.1	20.4	129.3	29.6	138.5	18.4	184.4	36.1	161.0	40.6
MY8	<i>Cecropia</i>	45.8	15.0	114.4	39.6	175.6	55.0	86.6	34.2	204.1	25.4	306.0	57.1	244.3	42.8	254.5	10.9
	<i>Cyathea</i>	113.3	41.9	94.2	28.8	130.8	39.5	108.1	15.3	236.6	2.6	242.5	10.6	279.7	22.3	320.8	33.5
	For. Soil	82.4	29.4	122.0	16.3	269.3	44.7	134.8	11.8	177.0	36.4	177.0	6.7	253.6	27.1	233.2	14.3
	Control	93.8	36.7	56.6	4.35	86.9	15.9	112.2	43.2	261.2	2.6	245.0	3.0	266.7	40.9	288.3	26.7
		102.2	58.5	81.2	27.4	209.1	75.4	93.1	32.7	202.2	11.9	255.3	30.3	389.2	135.9	240.6	9.4

APPENDIX Ib. Available soil P ( $\mu\text{g N g soil}^{-1}$ ) and soil pH, 0-10 cm depth (mean $\pm$ SE; n=3). T<sub>1</sub>=0 d (time of treatment additions); T<sub>2</sub>=60 d following treatment additions; T<sub>3</sub>=210 d following treatment additions; T<sub>4</sub>=370 d following treatment additions.

Landslide	Time Treatment	Avail P T <sub>1</sub>		Avail P T <sub>2</sub>		Avail P T <sub>3</sub>		Avail P T <sub>4</sub>		pH T <sub>1</sub>		pH T <sub>2</sub>		pH T <sub>3</sub>		pH T <sub>4</sub>	
		mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
ES10	<i>Cecropia</i>	0.77	0.06	0.61	0.23	0.80	0.15	0.48	0.22	4.40	0.13	4.37	0.03	4.33	0.06	4.50	0.05
	<i>Cyathea</i>	0.45	0.06	1.16	0.66	0.76	0.29	1.46	0.42	4.40	0.08	4.30	0.06	4.15	0.07	4.42	0.12
	For. Soil	1.25	0.75	0.53	0.12	0.96	0.12	0.75	0.34	4.47	0.02	4.23	0.02	4.12	0.03	4.30	0.08
	Fertilizer Control	0.81	0.43	0.83	0.41	0.67	0.12	0.38	0.11	4.52	0.04	4.17	0.10	4.18	0.03	4.58	0.09
J4	<i>Cecropia</i>	0.95	0.46	0.26	0.19	0.77	0.27	0.99	0.77	4.43	0.12	4.23	0.07	4.12	0.11	4.33	0.12
	<i>Cecropia</i>	0.88	0.44	0.00	0.00	0.52	0.43	8.89	7.98	4.75	0.13	4.75	0.13	4.30	0.29	4.63	0.10
	<i>Cyathea</i>	0.60	0.35	0.66	0.61	0.24	0.12	1.94	1.08	4.92	0.04	4.95	0.00	4.42	0.06	4.72	0.06
	For. Soil Fertilizer Control	0.84	0.48	0.29	0.04	0.20	0.11	1.89	0.46	4.80	0.10	4.68	0.16	4.27	0.09	4.68	0.09
ES5	<i>Cecropia</i>	0.17	0.17	1.67	1.28	0.68	0.46	0.71	0.43	4.83	0.02	4.60	0.05	4.23	0.03	4.68	0.04
	<i>Cecropia</i>	0.55	0.18	0.38	0.35	0.15	0.05	1.22	0.59	4.78	0.09	4.78	0.20	4.43	0.11	4.70	0.08
	<i>Cecropia</i>	0.55	0.12	0.90	0.51	1.29	0.10	1.09	0.87	5.30	0.20	5.08	0.23	5.32	0.24	5.30	0.25
	<i>Cyathea</i>	0.60	0.11	1.10	0.51	0.93	0.22	0.64	0.30	5.35	0.20	5.08	0.10	5.20	0.24	5.25	0.26
RB10	For. Soil Fertilizer Control	0.68	0.23	0.71	0.36	0.94	0.23	0.80	0.31	5.42	0.07	5.15	0.08	5.22	0.09	5.25	0.08
	<i>Cecropia</i>	0.40	0.22	1.28	0.68	1.54	0.39	2.67	0.79	5.30	0.13	4.92	0.12	5.30	0.18	5.10	0.13
	<i>Cecropia</i>	0.60	0.15	0.22	0.21	0.77	0.34	1.89	1.40	5.42	0.12	5.16	0.15	5.25	0.12	5.35	0.18
	<i>Cecropia</i>	7.35	0.55	8.43	0.53	7.58	0.62	5.57	0.63	5.03	0.04	5.23	0.04	4.98	0.02	5.08	0.03
MY8	<i>Cyathea</i>	6.67	0.49	7.08	0.41	7.07	0.77	5.08	0.85	5.02	0.03	5.10	0.05	4.92	0.02	4.98	0.02
	For. Soil Fertilizer Control	5.43	0.41	5.83	0.40	6.02	0.72	4.76	0.29	5.07	0.02	5.02	0.02	4.82	0.03	5.00	0.03
	<i>Cecropia</i>	6.67	0.71	8.20	1.05	7.05	0.86	4.78	0.34	5.05	0.00	4.75	0.11	4.70	0.03	4.97	0.02
	<i>Cecropia</i>	6.62	1.94	6.86	2.21	7.23	1.46	5.42	1.65	5.10	0.05	5.10	0.05	4.93	0.06	5.05	0.06
MY8	<i>Cecropia</i>	2.24	0.95	1.75	0.14	1.35	0.26	0.50	0.32	4.90	0.03	5.03	0.04	4.63	0.03	4.97	0.02
	<i>Cyathea</i>	1.81	0.30	2.18	0.18	1.93	0.42	1.69	0.84	4.95	0.03	5.10	0.05	4.65	0.03	4.87	0.02
	For. Soil Fertilizer Control	1.63	0.45	1.80	0.21	1.75	0.43	0.77	0.05	4.98	0.02	5.03	0.04	4.62	0.07	4.88	0.04
	<i>Cecropia</i>	1.50	0.15	5.50	2.34	2.58	1.61	1.11	0.26	4.95	0.00	4.70	0.20	4.43	0.10	4.85	0.06
		2.25	0.52	1.96	0.19	1.34	0.18	1.09	0.11	4.92	0.03	5.05	0.05	4.65	0.03	4.88	0.03

APPENDIX 1c. Soil organic matter (SOM) and gravimetric soil moisture (% dry mass), 0-10 cm depth (mean $\pm$ SE; n=3). T<sub>1</sub>=0 d (time of treatment additions); T<sub>2</sub>=60 d following treatment additions; T<sub>3</sub>=210 d following treatment additions; T<sub>4</sub>=370 d following treatment additions.

Landslide	Time	SOMPT <sub>1</sub>		SOMPT <sub>2</sub>		SOMPT <sub>3</sub>		SOMPT <sub>4</sub>		Moisture T <sub>1</sub>		Moisture T <sub>2</sub>		Moisture T <sub>3</sub>		Moisture T <sub>4</sub>		
		mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se	
ES10	Treatment																	
	<i>Cecropia</i>	14.71	2.58	15.80	1.66	16.68	2.01	16.05	1.45	32.85	3.72	47.04	2.68	48.81	3.54	29.26	5.42	
	<i>Cyathea</i>	16.37	0.57	16.46	0.18	16.88	0.40	17.70	0.58	35.25	4.45	49.25	4.07	47.83	5.36	35.14	5.21	
	For. Soil	16.44	0.69	17.29	0.70	17.55	0.64	17.16	0.85	31.40	5.46	46.57	4.02	45.10	6.23	30.71	2.25	
	Fertilizer Control	16.05	1.34	16.42	1.23	17.06	1.12	16.90	1.27	38.50	6.43	54.70	4.20	48.19	4.84	33.92	6.17	
J4	Treatment																	
	<i>Cecropia</i>	15.55	0.45	15.95	0.34	15.91	0.38	16.01	0.48	51.87	5.14	48.10	2.30	47.49	5.62	51.90	2.37	
	<i>Cyathea</i>	14.56	0.37	14.87	0.45	15.35	0.28	15.23	0.37	53.09	4.20	51.83	0.68	48.35	1.86	47.75	0.99	
	For. Soil	15.03	0.68	15.38	0.65	15.43	0.61	15.38	0.90	48.75	3.51	48.77	4.18	48.42	1.81	50.82	1.95	
	Fertilizer Control	14.58	0.63	14.59	0.71	15.05	0.75	15.00	0.76	52.65	2.74	49.99	1.91	51.28	3.86	48.75	1.74	
ES5	Treatment																	
	<i>Cecropia</i>	15.03	0.68	15.38	0.65	15.43	0.61	15.38	0.90	50.10	2.48	47.62	5.37	45.80	1.56	44.52	1.03	
	<i>Cyathea</i>	12.02	0.11	12.81	0.11	12.97	0.05	13.12	0.13	68.40	2.84	61.70	0.27	58.63	1.21	56.28	2.60	
	For. Soil	11.51	0.23	12.69	0.07	12.62	0.11	12.49	0.65	62.99	1.97	50.12	9.41	51.51	5.38	55.32	2.94	
	Fertilizer Control	11.92	0.15	12.84	0.17	12.29	0.19	12.76	0.18	65.07	3.33	55.95	5.60	52.11	3.77	53.89	6.67	
RB10	Treatment																	
	<i>Cecropia</i>	11.66	0.04	12.46	0.07	12.12	0.29	12.61	0.45	64.98	1.75	59.41	3.01	52.52	3.98	55.44	2.63	
	<i>Cyathea</i>	11.92	0.15	12.84	0.17	12.29	0.19	12.76	0.18	65.22	1.83	47.56	1.17	51.93	1.23	52.33	3.56	
	For. Soil	5.91	0.57	6.41	0.80	6.27	0.75	6.20	0.59	32.84	2.82	31.08	4.90	29.90	3.00	30.47	2.58	
	Fertilizer Control	6.86	0.32	6.91	0.43	6.37	0.50	6.82	0.35	36.10	1.93	33.92	3.49	30.71	4.23	33.05	3.34	
MY8	Treatment																	
	<i>Cecropia</i>	6.15	0.49	6.88	0.79	6.97	0.47	7.02	0.52	36.48	0.64	33.88	0.89	32.10	3.22	34.33	1.82	
	<i>Cyathea</i>	6.23	0.08	5.80	0.04	6.20	0.53	5.81	0.24	31.70	0.59	32.17	0.33	30.17	1.91	31.30	2.05	
	For. Soil	5.62	0.48	5.54	0.42	5.64	0.44	5.49	0.14	30.43	1.78	28.35	2.30	27.12	1.23	28.74	1.26	
	Fertilizer Control	7.95	0.10	8.43	0.28	8.51	0.10	8.01	0.35	40.70	0.80	36.43	0.98	37.43	1.27	35.94	0.65	
MY8	Treatment																	
	<i>Cecropia</i>	7.78	0.59	8.19	0.73	8.27	0.82	7.34	0.63	40.98	3.43	35.10	1.14	32.65	2.11	34.73	0.71	
	<i>Cyathea</i>	7.28	0.34	8.50	0.09	7.67	0.04	7.92	0.47	41.33	2.94	34.62	1.11	28.80	3.79	38.23	1.37	
	For. Soil	7.72	0.34	8.50	0.09	7.67	0.04	7.92	0.47	41.33	2.94	34.62	1.11	28.80	3.79	38.23	1.37	
	Fertilizer Control	7.28	0.59	8.19	0.73	8.27	0.82	7.34	0.63	44.46	3.09	37.55	3.45	41.10	6.75	43.18	0.20	

## BIBLIOGRAPHY

- Aide, T.M., and J. Cavelier. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* 2: 219-229.
- Adams, P.W., and R.C. Sidle. 1987. Soil conditions on three recent landslides in S.E. Alaska. *Forest Ecology and Management* 18: 93-102.
- Alpkem Corporation. 1992. The Flow Solution Operation Manual. Alpkem Corporation, Wilsonville, Oregon.
- Augspurger, C.K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* 72: 777-795.
- Augspurger, C.K., and S.F. Franson. 1988. Input of wind-dispersed seeds into light-gaps and forest sites in a Neotropical forest. *Journal of Tropical Ecology* 4: 239-252.
- Baker, H.G. 1972. Seed weight in relation to environmental conditions in California. *Ecology* 53: 997-1010.
- Barbour, M.G., J.H. Burk, W.D. Pitts, F.S. Gillman, and M.W. Schwartz. 1999. Benjamin/Cummings, Menlo Park, California.
- Berendse, F., E.J. Lamments, and H. Olf. 1998. Soil organic matter accumulation and its implications for nitrogen mineralization and plant species composition during succession in coastal dune slacks. *Plant Ecology* 137: 71-78.
- Binkley, D., and P. Vitousek. 1989. Soil nutrient availability. Pages 75-96 in R.W. Pearcy, J.R. Ehleringer, H.A. Mooney and P.W. Rundel, editors. *Plant Physiological Ecology*. Chapman and Hall, New York.
- Bloomfield, J., K.A. Vogt, and D.J. Vogt. 1993. Decay rate and substrate quality of fine roots and foliage of tropical tree species in the Luquillo Experimental Forest, Puerto Rico. *Plant and Soil* 150: 233-245.
- Boccheciamp, R.A. 1977. Soil survey of the Humacao area of eastern Puerto Rico. United States Department of Agriculture, Soil Conservation Service. Washington, D.C.



- Bollen, W.B. 1953. Mulches and soil conditions. Carbon and nitrogen in farm and forest products. *Agricultural and Food Chemistry* 7: 379-381.
- Bray, R.H., and L. Kurtz. 1945. Determination of total, organic, and available forms of phosphorus in soils. *Soil Science* 59: 39-45.
- Brokaw, N.V.L. 1998. *Cecropia schreberiana* in the Luquillo Mountains of Puerto Rico. *The Botanical Review* 64: 91-120.
- Brown, S., A.E. Lugo, S. Silander, and L. Liegel. 1983. Research history and opportunities in the Luquillo Experimental Forest. United States Forest Service General Technical Report. SO-44. Washington D.C.
- Calderón-González, F. 1993. The role of mycorrhizae in the nutrient absorptive strategy of important landslide colonizers. MSc Thesis. University of Puerto Rico, Río Piedras.
- Campell, B.M., T. Lynman, and J.C. Hatton. 1990. Small-scale patterning in the recruitment of forest species during succession in tropical dry forest, Mozambique. *Vegetatio* 87: 51-57.
- Carreiro, M.M., R.L. Sinsabaugh, D.A. Repert, and D.F. Parkhurst. 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. *Ecology* 81: 2359-2365.
- Chapin, F.S., III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11: 233-260.
- Chapin, F.S., III. 1995. New cog in the nitrogen cycle. *Nature* 377: 199-200.
- Chazdon, R.L., and N. Fetcher. 1984. Light environments of tropical forest. Pages 27-36 in E. Medina, H.A. Mooney, and C. Vázquez-Yanes, editors. *Physiological ecology of plants in the wet tropics*. Dr. W. Junk, Boston, Massachusetts.
- Chiariello, N.R., H.A. Mooney, and K. Williams. 1989. Plant physiological ecology: field methods and instrumentation. Pages 327-365 in R.W. Pearcy, J.R. Ehleringer, H.A. Mooney, and P.W. Rundel, editors. Chapman and Hall, New York.
- Cooperband, L.R., R.E.J. Boerner, T.J. Logan. 1994. Humid tropical leguminous tree and pasture grass responsiveness to vesicular-arbuscular mycorrhizal infection. *Mycorrhiza* 4: 233-239.
- Coûteaux, M.-M., M. Mousseau, M.-L. Célérier, and P. Bottner. 1991. Increased atmospheric CO<sub>2</sub> and litter quality: decomposition of sweet chestnut leaf litter with animal food webs of different complexities. *Oikos* 61: 54-64.

- Cuenca, G., and M. Lovera. 1992. Vesicular-arbuscular mycorrhizae in disturbed and revegetated sites from La Gran Sabana, Venezuela. *Canadian Journal of Botany* 70: 73-79.
- Dalling, J.W., and E.V.J. Tanner. 1995. An experimental study of regeneration on landslides in montane rain forest in Jamaica. *Journal of Ecology* 83: 55-64.
- Denslow, J.S., and A.E. Gomez Diaz. 1990. Seed rain to tree-fall gaps in a Neotropical rain forest. *Canadian Journal of Forest Research* 20: 642-648.
- Denslow, J.S., J.C. Schultz, P.M. Vitousek, and B.R. Strain. 1990. Growth responses of tropical shrubs to treefall gap environments. *Ecology* 71: 165-179.
- Devoe, N.N. 1989. Differential seedling and regeneration in openings and beneath closed canopy in sub-tropical wet forest. Ph.D. Dissertation. Yale University, New Haven, Connecticut.
- Everham, E.M., R.W. Myster, and E. VanDeGenachte. 1996. Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *American Journal of Botany* 83: 1063-1068.
- Ewel, J.J., and J.L. Whitmore. 1973. The ecological life zones of Puerto Rico and the Virgin Islands. United States Forest Service Research Paper. ITF-18. Institute of Tropical Forestry, Rio Piedras, Puerto Rico.
- Ewel, J., C. Berish, B. Brown, N. Price, and J. Raich. 1981. Slash and burn impacts on a Costa Rican wet forest site. *Ecology* 62: 816-829.
- Ewel, J., M. Mazzarinno, and C. Berish. 1991. Tropical soil fertility changes under monocultures and successional communities of different structure. *Ecological Applications* 1: 289-302.
- Fenner, M. 1985. *Seed Ecology*. Chapman and Hall, New York.
- Fernández, 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.
- Fetcher, N., B.L. Haines, R.A. Cordero, D.J. Lodge, L.R. Walker, D.S. Fernández, and W.T. Lawrence. 1996. Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. *Journal of Ecology* 84: 331-341.
- Fogel, R., and K. Cromack, Jr. 1977. Effect of habitat and substrate quality on Douglas fir litter decomposition in Western Oregon. *Canadian Journal of Botany* 55: 1632-1640.

- Foster, R.B. 1982. The seasonal rhythm of fruitfall on Barro Colorado Island. Pages 67-81 in E.G. Leigh, A.S. Rand and D.M. Windsor, editors. *The Ecology of a Tropical Forest*. Smithsonian Institution Press, Washington, D.C.
- Foth, H.D., and B.G. Ellis. 1997. *Soil Fertility*, 2<sup>nd</sup> Edition. Lewis Publishers. New York.
- Frizano, J., A.H. Johnson, D.R. Vann, and F.N. Scatena. 2002. Soil phosphorus fractionation during forest development on landslide scars in the Luquillo Mountains, Puerto Rico. *Biotropica* 34: 17-26.
- Gallardo, J.F., J. Saavedra, T.Martin-Patino, and A. Milan. 1987. Soil organic matter determinations. *Communications in Soil Science and Plant Analysis* 18: 699-707.
- Garwood, N.C., D.P. Janos, and N. Brokaw. 1979. Earthquake-caused landslides: A major disturbance to tropical forests. *Science* 205: 997-999.
- González, G., and T.R. Seastedt. 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* 82: 955-964.
- Guariguata, M.R. 1990. Landslide disturbance and forest regeneration in the Upper Luquillo Mountains. *Journal of Ecology* 78: 814-832.
- Guevara, S., S.E. Purata, and E. Van der Maarel. 1986. The role of remnant forest trees in tropical secondary succession. *Vegetatio* 66: 77-84.
- Hallawachs, W. 1986. *Agoutis (Dasyprocta punctata)*, the inheritors of guapinol (*Hymenaea courbaril*: Leguminosae). Pages 285-304 in A. Estarda and T.H. Fleming, editors. *Frugivores and Seed Dispersal*. Dr. W. Junk, Dordrecht, The Netherlands.
- Hendershot, W.H. and H. Lalonde. 1993. Soil reaction and exchangeable acidity. Pages 141-142 in M.R. Carter, editor. *Soil Sampling Methods of Analysis*. Lewis Publishers, Boca Raton, Florida.
- Herbert, D.A., and J.H. Fownes. 1995. Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil. *Biogeochemistry* 29: 223-235.
- Heyne, C.M. 2000. Soil and vegetation recovery on abandoned paved roads in a humid tropical rain forest, Puerto Rico. M.Sc. Thesis. University of Nevada, Las Vegas. Las Vegas, Nevada.
- Higuchi, T. 1985. *Biosynthesis and Biodegradation of Wood Components*. Academic Press, Inc., Orlando, Florida.

- Hilhorst, H.W.M., and C.M. Karssen. 2000. Effect of chemical environment on seed germination. Pages 293-309 in M. Fenner, editor. *Seeds: The ecology of regeneration in plant communities*, 2<sup>nd</sup> Edition. CABI Publishing, New York.
- Holl, K.D. 1998. Do perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? *Restoration Ecology* 6: 253-261.
- Hoppes, W.G. 1988. Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology* 69: 320-329.
- Howard, P.J.A., and D.M. Howard. 1990. Use of organic carbon and loss-on-ignition to estimate soil organic matter in different soil types and horizons. *Biology and Fertility of Soils* 9: 306-310.
- Howe, H.F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.
- Hutson, M.A., and T.M. Smith. 1987. Plant succession: life history and competition. *American Naturalist* 130: 168-198.
- Jackson, J.F. 1981. Seed size as a correlate of temporal and spatial patterns of seed fall in a neotropical forest. *Biotropica* 13: 121-130.
- Janos, D.P. 1980. Mycorrhizae influence tropical succession. *Biotropica Supplement* 12: 56-64.
- Janzen, D.H. 1988. Management of habitat fragments in a tropical dry forest: growth. *Annals of the Missouri Botanic Garden* 75: 105-116.
- Jenny, H. 1980. *The Soil Resource*. Springer-Verlag, New York.
- JMP. 2000. SAS Institute, Inc. North Carolina.
- Jordano, P. 2000. Fruits and frugivory. Pages 125-165 in M. Fenner, editor. *Seeds: The Ecology of Regeneration in Plant Communities*, 2<sup>nd</sup> Edition. CABI Publishing, New York.
- Kandeler, E. 1996. N-mineralization under aerobic conditions. Pages 139-141 in F. Schinner, R. Ölinger, E. Kandeler, and R. Margesin, editors. *Methods in Soil Biology*. Springer-Verlag, Berlin, Germany.
- Karam, A. 1993. Chemical Properties of Organic Soils. Pages 461-463 in M.R. Carter, editor. *Soil Sampling Methods of Analysis*. Lewis Publishers, Boca Raton, Florida.
- Kielland, K. 1994. Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. *Ecology* 75: 2373-2383.

- Kuo, S. 1996. Phosphorus. Pages 894-895 in D.L. Sparks, editor. *Methods of Soil Analysis. Part 3, Chemical Methods*. Soil Science Society of America and American Society of Agronomy, Madison, Wisconsin.
- La Caro, F., and R.L. Rudd. 1985. Leaf litter decomposition rates in Puerto Rican montane rain forest. *Biotropica* 17: 269-276.
- Larsen, M.C., and A. Simon. 1993. A rainfall intensity-duration threshold for landslides in a humid-tropical environment, Puerto Rico. *Geografiska Annaler* 75A: 13-23.
- Larsen, M.C., and A.J. Torres-Sánchez. 1990. Rainfall-soil moisture relations in landslide-prone areas of a tropical rain forest, Puerto Rico. *International Symposium of Tropical Hydrology and Fourth Caribbean Islands Water Resources Congress*, San Juan, Puerto Rico, July 23-27.
- Larsen, M.C. and A.J. Torres-Sánchez. 1996. Geographic relations of landslide distribution and assessment of landslide hazards in the Blanco, Cibuco, and Coamo Basins, Puerto Rico. *United States Geological Survey Report 95-4029*. San Juan, Puerto Rico.
- Lawrence, W.T. 1996. Plants: The food base. Pages 18-51 in D.P Reagan and R.B. Waide, editors. *The Food Web of a Tropical Rain Forest*. The University of Chicago Press, Chicago, Illinois.
- Levey, D.J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58: 251-269.
- Lewis, S.L., and E.V.J. Tanner. 2000. Effects of above- and belowground competition on growth and survival of rain forest tree seedlings. *Ecology* 81: 2525-2538.
- Liogier, H.A., and Martorell, L.F. 1982. *Flora of Puerto Rico and adjacent islands: a systematic synopsis*. Editorial de la Universidad de Puerto Rico, Río Piedras, Puerto Rico.
- Little, E.L., R.O. Woodbury, and F. H. Wadsworth. 1974. *Trees of Puerto Rico and the Virgin Islands, 2<sup>nd</sup> Volume*. United States Department of Agriculture, United States Forest Service.
- Lodge, D.J., F.N. Scatena, C.E. Asbury, and M.J. Sanchez. 1991. Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rain forest of Puerto Rico. *Biotropica* 23: 336-342.
- MacKinnon, J.R., and MacKinnon, K.S. 1978. Comparative feeding ecology of six primates in West Malaysia. Pages 302-321 in D.J. Chivers and J. Herbert, editors. *Recent Advances in Primatology, Vol. 1*. Academic Press, London, England.

- Marchiol, L., C. Mondini, L. Leita, and G. Zerbi. 1999. Effects of municipal waste leachate on seed germination in soil-compost mixtures. *Restoration Ecology* 7: 155-161.
- McDonnell, M.J. 1986. Old field vegetation height and dispersal pattern of bird disseminated woody plants. *Bulletin of the Torrey Botanical Club* 113: 6-11.
- McDonnell, M.J., and E.W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56: 109-116.
- McClanahan, T.R., and R.W. Wolfe. 1993. Accelerating forest succession in fragmented landscapes: the role of birds and perches. *Conservation Biology* 7: 279-288.
- McLean, E.O. 1982. Soil pH and lime requirement. Pages 199-224 in A.L. Page, R.H. Miller, and D.R. Keeney, editors. *Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties, 2<sup>nd</sup> Edition*. American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin, USA.
- Melillo, J.M., J.D. Aber, and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63: 621-626.
- Milliken, G.A., and D.E. Johnson. 1992. *Analysis of Messy Data, Vol. I: Designed Experiments*. Chapman and Hall, New York.
- Murray, K.G. 1988. Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs* 58: 271-298.
- Myster, R.W. 1997. Seed predation, disease and germination on landslides in Neotropical lower montane wet forest. *Journal of Vegetation Science* 8: 55-64.
- Myster, R.W., and D.S. Fernández. 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.
- Myster, R.W., and R.O. Sarmiento. 1998. Seed inputs to microsite patch recovery on two Tropicandean landslides in Ecuador. *Restoration Ecology* 6: 35-43.
- Nelson, D.M., and L.E. Sommers. 1996. Total carbon, organic carbon, and organic matter. Pages 1002-1010 in D.L. Sparks, editor. *Methods of Soil Analysis. Part 3, Chemical Methods*. American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin.

- Nepstad, D., C. Uhl, and E.A.S. Serrao. 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Para, Brazil. Pages 215-229 in A.B. Anderson, editor. *Alternatives to Deforestation: Steps toward Sustainable USE of the Amazon Rain Forest*. Columbia University Press, New York.
- Newman, E.I. 1995. Phosphorus inputs to terrestrial ecosystems. *Journal of Ecology* 83: 713-726.
- Nziguheba, G., C.A. Palm, R.J. Buresh, and P.C. Smithson. 1998. Soil phosphorus fractions and adsorption as affected by organic and inorganic sources. *Plant and Soil* 198: 159-168.
- Olsen, S.R., and L.E. Sommers. 1982. Phosphorus. Pages 416-417 in A.L. Page, R.H. Miller, and D.R. Keeney, editors. *Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties, 2<sup>nd</sup> Edition*. American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin.
- Orozco Segovia, A. 1986. Fisiología ecológica del fotoblastismo en semillas de cuatro especies del género *Piper* L. Ph.D. Dissertation, Universidad Nacional Autónoma de Mexico, D.F.
- Popma, J., and F. Bongers. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* 75: 625-632.
- Proctor, G.R. 1989. Ferns of Puerto Rico and the Virgin Islands. *Memoirs of the New York Botanical Garden*, Volume 53.
- Raffaele, H.A. 1989. Birds of Puerto Rico and the Virgin Islands. Princeton University Press, New Jersey.
- Ranney, R.W. 1969. An organic carbon-organic matter conversion equation for Pennsylvania surface soils. *Soil Science Society of America Proceedings* 33: 809-811.
- Reever Morghan, K.J., and T.R. Seastedt. 1999. Effects of soil nitrogen reduction on nonnative plants in restored grasslands. *Restoration Ecology* 7: 51-55.
- Restrepo, C., and P. Vitousek. 2001. Landslides, alien species, and the diversity of a Hawaiian montane mesic ecosystem. *Biotropica* 33: 409-420.
- Roberts, R.D., and J.M. Roberts. 1986. The selection and management of soils in landscape schemes. Pages 99-126 in A.D. Bradshaw, D.A. Goode, and E.H.P. Thorpe, editors. *Ecology and Design in Landscape*. Blackwell, Oxford.

- Salinas, J.G., J.I. Sanz, and E. Sieverding. 1985. Importance of VA mycorrhizae for phosphorus supply to pasture plants in tropical Oxisols. *Plant and Soil* 84: 347-360.
- Sanchez, P.A. 1976. *Properties and Management of Soils in the Tropics*. John Wiley and Sons, New York.
- SAS Institute. 1996. *SAS Procedures Guide, Version 6.19*. SAS Institute, Cary, North Carolina.
- Scatena, F.N., W. Silver, T. Siccama, A. Johnson, and M.J. Sanchez. 1993. Biomass and nutrient content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. *Biotropica* 25: 15-27.
- Schemske, D.W., and N. Brokaw. 1981. Treefalls and the distribution of understory birds in a tropical forest. *Ecology* 62: 938-945.
- Schimpf, D.J., and I.G. Palmald. 1980. Germination response of weed seeds to soil nitrate and ammonium with and without simulated overwintering. *Weed Science* 28: 190-193.
- Schlesinger, W.H. 1997. *Biogeochemistry: An Analysis of Global Change*. Academic Press, New York.
- Seiders, V.M. 1971. Geologic map of the El Yunque quadrangle, Puerto Rico. United States Geologic Survey Map I-658. United States Government Printing Office, Washington, D.C.
- Sheldrick, B.H., and C. Wang. 1993. Particle size distribution. Pages 507-509 in M.R. Carter, editor. *Soil Sampling Methods of Analysis*. Lewis Publishers, Boca Raton, Florida.
- Silver, W.L., and K.A. Vogt. 1993. Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. *Journal of Ecology* 8: 729-738.
- Silver, W.L., F.N. Scatena, T.G. Siccama, and M.J. Sánchez. 1994. Nutrient availability in a montane wet tropical forest: Spatial patterns and methodological considerations. *Plant and Soil* 164: 129-145.
- Silver, W.L., F.N. Scatena, A.H. Johnson, T.G. Siccama, and F. Watt. 1996. At what temporal scales does disturbance affect belowground nutrient pools? *Biotropica* 28: 441-457.
- Singh, K.P. 1969. Studies in decomposition of leaf litter of important trees of tropical deciduous forests at Varanasi. *Tropical Ecology* 10: 292-311.



- Slocum, M.G. 2001. How tree species differ as recruitment foci in a tropical pasture. *Ecology* 82: 2547-2559.
- Snow, B.K., and D.W. Snow. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. *Auk* 88: 291-322.
- Soil Survey Staff. 1995. Order 1 Soil Surveys of Luquillo Long-Term Ecological Research Grid, Puerto Rico. United States Department of Agriculture. Natural Resource Conservation Service.
- Sollins, P. 1998. Factors influencing species composition in tropical lowland rain forest: Does soil matter? *Ecology* 79: 23-30.
- Sollins, P., G.P. Robertson, and G. Uehara. 1988. Nutrient mobility in variable- and permanent-charge soils. *Biogeochemistry* 6: 181-199.
- Sparks, D.L. 1995. *Environmental Soil Chemistry*. Academic Press, New York.
- Sprent, J.I. 1987. *The Ecology of the Nitrogen Cycle*. Cambridge University Press, Cambridge.
- Steel, R.D., and Torrie, J.H. 1980. *Principles and Procedures of Statistics*, 2<sup>nd</sup> Edition. McGraw-Hill, New York.
- Steinbauer, G.P., and B. Grigsby. 1957. Interaction of temperature, light, and moistening agent in the germination of weed seeds. *Weeds* 5: 157.
- Swift, M.J., O.W. Heal, and J.M. Anderson. 1979. *Decomposition in Terrestrial Ecosystems*. Blackwell Scientific Publications. Oxford.
- Taylor, C.M. 1994. *Annotated Checklist of the Flowering Plants of the El Verde Field Station, Puerto Rico*. University of Puerto Rico.
- Tiessen, H., E. Cuevas, and P. Chacon. 1994. The role of soil organic matter in sustaining soil fertility. *Nature* 371: 783-785.
- Tillman, D. 1988. *Plant strategies and the structure and dynamics of plant communities*. Princeton University Press, Princeton, New Jersey.
- Toh, I., M. Gillespie, and D. Lamb. 1999. The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. *Restoration Ecology* 7: 288-297.
- Topp, G.C. 1993. Soil water content. Pages 542-544 in M.R. Carter, editor. *Soil Sampling Methods of Analysis*. Lewis Publishers, Boca Raton, Florida.

- Turner, I.M., N.D. Brown, A.C. Newton. 1993. Effects of fertilizer application on dipterocarp seedling growth and mycorrhizal infection. *Forest Ecology and Management* 57: 329-337.
- Uehara, G., and G.G. Gillman. 1981. The mineralogy, chemistry, and physics of tropical soils with variable charge clays. Westview, Boulder, Colorado.
- Uhl, C., and K. Clark. 1983. Seed ecology of selected Amazon Basin successional species. *Botanical Gazette* 144: 419-425.
- Uhl, C., and C.F. Jordan. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. *Ecology* 65: 1476-1490.
- Uhl, C., K. Clark, N. Dezzeo, and P. Maquirino. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69: 751-763.
- United States Department of Agriculture. 1996. Peroxide digestion gravimetric weight loss. *Soil Survey Laboratory Methods Manual, Soil Survey Investigations Report No. 42, Version 3.0.*
- Varnes, D.J. 1978. Slope movement types and processes. *Landslides: Analysis and Control*. Pages 11-33 in R.L. Schuster and R.S. Krizek, editors. Special Report. 176. United States National Academy of Sciences Transportation Research Board, Washington, D.C.
- Vitousek, P.M. 1984. Litterfall nutrient cycling and nutrient limitation in tropical forest. *Ecology* 65: 285-298.
- Vitousek, P.M., and P.A. Matson. 1984. Mechanisms of nitrogen retention in forest ecosystems: a field experiment. *Science* 225: 51-51.
- Vitousek, P.M., and R.L. Sanford, Jr. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17: 137-167.
- Vitousek, P.M., and H. Farrington. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biogeochemistry* 37: 63-75.
- Vogt, K.A., C.C. Grier, and D.J. Vogt. 1986. Production turnover, and nutrient dynamics of above- and belowground detritus of world forest. *Advanced Ecological Research* 15: 303-377.
- von Ende, C.N. 1993. Repeated-measures analysis: Growth and other time-dependent measures. Pages 113-137 in S.M. Scheiner and J. Gurevitch, editors. *Design and Analysis of Ecological Experiments*. Chapman and Hall, New York.

- Waide, R.B. 1991. The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23: 475-480.
- Waide, R.B., and A.E. Lugo. 1992. A research perspective on disturbance and recovery of a tropical montane forest. Pages 173-190 in J. Goldammer, editor. *Tropical forest in transition: Ecology of natural and anthropogenic disturbance processes*. Berkhauser-Verlag.
- Waide, R.B. 1996. Birds. Pages 363-398 in D.P. Reagan and R.B. Waide, editors. *The Food Web of a Tropical Rain Forest*. The University of Chicago Press, Chicago, Illinois.
- Walker, L.R. 1994. Effects of fern thickets on woodland development on landslides in Puerto Rico. *Journal of Vegetation Science* 5: 525-532.
- Walker, L.R., and L. Neris. 1993. Posthurricane seed rain dynamics in Puerto Rico. *Biotropica* 25: 408-418.
- Walker, L.R., and W. Boneta. 1995. Plant and soil responses to fire on a fern-covered landslide in Puerto Rico. *Journal of Tropical Ecology* 11: 473-479.
- Walker, L.R., D.J. Zarin, N. Fetcher, R.W. Myster, and A.H. Johnson. 1996. Ecosystem development and plant succession on landslides in the Caribbean. *Biotropica* 28: 566-576.
- Walker, T.W., and J.K. Syers. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15: 1-19.
- Wetmore, A. 1916. *Birds of Puerto Rico*. United States Department of Agriculture Bulletin 326. United States Government Printing Office, Washington, D.C.
- Wiley, J.W., and G.P. Bauer. 1985. Caribbean National Forest, Puerto Rico. *American Birds* 39: 12-18.
- Willig, M.R., and M.R. Gannon. 1996. Mammals. Pages 399-433 in D.P. Reagan and R.B. Waide, editors. *The Food Web of a Tropical Rain Forest*. The University of Chicago Press, Chicago, Illinois.
- Willson M.F., and F.H.J. Crome. 1989. Patterns of seed rain at the edge of a tropical Queensland rain forest. *Journal of Tropical Ecology* 5: 301-308.
- Windsor, D.M., and A.M. Clements. 2001. A germination and establishment field trial of *Themeda australis* (kangaroo grass) for mine site restoration in the central tablelands of New South Wales. *Restoration Ecology* 9: 104-110.

- Wunderle, J.M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99: 223-235.
- Wunderle, J.M., A. Diaz, I. Velazquez, and R. Scharrón. 1987. Forest openings and the distribution of understory birds in a Puerto Rican rainforest. *Wilson Bulletin* 99: 22-37.
- Young, K.R., J.J. Ewel, and B.J. Brown. 1987. Seed dynamics during forest succession in Costa Rica. *Vegetatio* 71: 157-173.
- Zarin, D.J., and A.H. Johnson. 1995. Nutrient accumulation during primary succession in montane tropical forest, Puerto Rico. *Soil Science Society of America* 59: 1444-1452.
- Zimmerman, J.K., W.M. Pulliam, D.J. Lodge, V. Quinones-Orfila, N. Fetcher, S. Guzmán-Grajales, J.A. Parrotta, C.E. Asbury, L.R. Walker, and R.B. Waide. 1995. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. *Oikos* 72: 314-322.
- Zink, T.A., and M.F. Allen. 1998. The effects of organic amendments on the restoration of a disturbed coastal sage scrub habitat. *Restoration Ecology* 6: 52-58.

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