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Organic matter inputs create variable resource patches on Puerto Rican landslides

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Abstract

Landslides are a frequent disturbance in montane tropical rainforests that result in heterogeneous environments for plant and soil development. Natural inputs of organic matter and associated nutrients contribute to soil fertility patchiness within landslides. To test the importance of organic matter and nutrient addition to landslide soil fertility and plant growth, we mixed three types of organic matter substrates that are common to landslides (*Cecropia* leaves, *Cyathea* fronds, and forest soil) and commercial fertilizer into recently eroded soil on five landslides in Puerto Rico. In addition, we sowed seeds of two common landslide colonists (*Paspalum* and *Phytolacca*) into the soil treatment plots in order to test treatment effects on seed germination and seedling growth. Soils, seed germination, and seedling growth were monitored for one year and the field experiment was replicated in a one-year screen-house experiment. Despite highly variable initial landslide conditions, responses to soil treatments were similar across all five landslides. The forest soil addition increased total soil nitrogen and soil organic matter on landslides within 60 days, whereas *Cecropia* leaves provided increased soil organic matter only after 210 days. Commercial fertilizer increased plant-available soil nitrogen and phosphorus within 60 days, and also increased seed germination of *Paspalum* seeds when compared to soils treated with *Cecropia* leaves. Despite these positive effects of treatments on soils and germination, there were no treatment effects on seedling growth in the field, perhaps due to leaching or other losses of soil nutrients evident in the lack of significant treatment differences in soil resources at 370 days. In the screen-house, forest soil and commercial fertilizer treatments significantly increased soil fertility and seedling growth of both *Paspalum* and *Phytolacca* compared to control treatments. These different responses to three common types of organic matter inputs create patchy soil conditions with important implications for plant colonization and landslide succession.

Introduction

Landslides, often triggered by high rainfall (Larsen and Simon 1993), are one of the most severe disturbances in tropical montane forests because of the partial or total loss of vegetation and topsoil (Garwood et al. 1979; Walker et al. 1996; Restrepo and Vitousek 2001). The mass movement of soil, vegetation, and litter during a landslide dramatically alters such ecosystem properties and processes as microclimate (Fernández and Myster 1995; Fetcher et al. 1996), soil nutrients and organic matter (Guariguata 1990; Walker et al. 1996), surface runoff (Larsen and Torres-Sánchez 1990), seed dispersal (Shiels and Walker 2003) and vegetation (Walker 1994). These alterations vary in severity, both across and within landslides, creating patches of widely ranging fertility that strongly influence the process of biotic recovery (Pickett and White 1985; Pickett et al. 1999). How the spatial heterogeneity of resources on landslides impacts succession is not clear.

Variable patterns of plant colonization further increase landslide heterogeneity by adding both spatial and temporal gradients (van Coller et al. 2000). Preferential colonization of the nutrient-rich lower edges of landslides over the nutrient-poor slip face at the upper edges of landslides (Guariguata 1990; Walker and Neris 1993) suggests that organic matter and soil nutrients are limiting factors in landslide succession (Walker et al. 1996). Organic matter from landslides comes from forest vegetation and soils incorporated into the landslide soil or later transported onto the landslide from subsequent erosion. Litterfall is an additional source of organic matter and it comes from new plant growth on the landslide, plants that survived the initial disturbance *in situ*, or plants in the surrounding forests. The few studies that have experimentally examined the effects of soil fertility on landslide succession (Dalling and Tanner 1995; Fetcher et al. 1996) used either commercial fertilizer or manure and concur that plant growth on tropical landslides is limited by soil nutrients. However, the link between natural inputs of organic matter and soil fertility has not been examined. In this study, we compare the impacts of additions of commercial fertilizer, forest soil and leaves of two colonizing plant species on soil fertility and plant growth.

Methods

Study site

This study was conducted on five landslides in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (18°18′ N, 65°50′ W) where mean annual precipitation is 3000–4000 mm with high year-to-year variation and little seasonality. Mean monthly temperatures range from 21 to 25 °C (Brown et al. 1983; Soil Survey Staff 1995). The landslides used in this study were between 460 and 750 m a.s.l (Table 1). Below 600 m elevation the vegetation is subtropical wet forest (Ewel and Whitmore 1973), characterized by tabonuco (*Dacryodes excelsa*), ausubo (*Manilkara bidentata*), and motillo (*Sloanea berteriana*) trees. Above 600 m, the vegetation is subtropical rain forest, characterized by palo colorado (*Cyrilla racemiflora*) and patches of palm (*Prestoea montana*) (Waide and Lugo 1992). Vegetation 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, Miconia*, and *Tabebuia*. A more detailed description of landslide vegetation in the LEF is found in Walker (1994), Walker et al. (1996), and Myster and Walker (1997).

We 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^2, and that were accessible (< 500 m from a road or trail). Soils in two landslides (RB10 and MY8) were Inceptisols derived from quartz-diorite bedrock, and the other three landslides (ES5, ES10, J4) were Ultisols derived from volcaniclastic bedrock (Seiders 1971; Table 1). Landslides were defined by watersheds (Río Espíritu Santo = ES, Jiménez = J, Río Blanco = RB, and Río Mameyes = MY, and numbers used in other landslide studies, e.g., see Walker and Neris 1993; Shiels and Walker 2003; Shiels in press). Both soil types are

Table 1. Site characteristics for the five landslides used for the field experiment in the LEF, Puerto Rico.

Site	Soil parent material	Elevation (m a.s.l.)	Area (m^2)	Aspect	Slope (°)	Light (μ Einsteins m^{-2} s^{-1})
ES5	Volcaniclastic	580	2923	NW	14	2267
ES10	Volcaniclastic	600	1440	NE	21	1750
J4	Volcaniclastic	460	1457	NW	23	2050
RB10	Quartz-diorite	600	810	E	15	1867
MY8	Quartz-diorite	750	1512	NE	27	2167

Light was determined (using a LI-Cor Quantum Sensor Model LI-185B) at ground level by averaging three measurements taken between noon and 2 pm local time on a day with < 10% cloud cover.

acidic, silty clay loams that have low permeability and high susceptibility to slippage (Boccheciamp 1977).

Soil treatments and experimental design

Five soil treatments (senesced leaves of *Cecropia schreberiana* Miq. (Moraceae), senesced leaves of *Cyathea arborea* (L.) J.E. Sm. (Cyatheaceae), forest soil, commercial fertilizer, control) 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 soils, seeds, and seedlings. The organic matter treatments (*Cecropia, Cyathea*, forest soil) were chosen because they represent common substrate inputs to landslides in the LEF (Walker et al. 1996; Shiels in press). *Cecropia* is the most common woody species occurring on LEF landslides (Myster and Walker 1997) and is one of the 10 most common tree species in the LEF (Brokaw 1998). Therefore, *Cecropia* leaves may be deposited into landslides from individuals within the landslide or from those surrounding the landslide. *Cyathea* is also one of the most common plant colonists to landslides (Guariguata 1990; Walker et al. 1996) and often dominants the landslide overstory in early succession (L. Walker unpublished data). Therefore, *Cyathea* is an organic matter source originating from within the landslide and not the surrounding forest. Forest soil can remain (often in patches) after the initial landslide occurs, or it can enter into the landslide from the surrounding forest by post-landslide erosion (A. Shiels unpublished data). The commercial fertilizer is a nutrient addition absent of organic matter, and therefore was used as a comparison to the 'natural' organic matter inputs.

Treatment quantities were determined by referencing past literature for the study site such that three times the total nitrogen (N) found in annual non-hurricane litterfall in the El Verde portion of the LEF (Lodge et al. 1991) was used as the basis of all treatments. This amounted to 19.5 g N m^{-2} (1296 g litter m^{-2} year^{-1}). Total dry mass of each treatment was then calculated and applied in a one-time addition in the following quantities: For both *Cecropia* and *Cyathea*, 1300 g m^{-2} of senesced, dried, and cut-up leaves (ca. 2 cm^{2} pieces) were added in ratios equaling their natural leaf-fall (*Cecropia*: 21.5% petiole, 78.5% g blade; *Cyathea*: 66.5% rhachis, 33.5% pinnae; Shiels 2002). Forest soil, collected from the top 5 cm of soil after removing the O-horizon, was added field moist and unsterilized at 3900 g m^{-2} (6100 g m^{-2} wet). Fertilizer (108 g m^{-2} of Dynamite Plant Food$^{\text{TM}}$ polymer-resin coated, 6-month, time-release) had the following nutrient content: total N 18% (8.6% as NH_4, 9.4% as NO_3), available phosphorus (P as P_2O) 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%. Reference samples of each organic matter treatment-substrate were taken to more accurately determine total N concentrations, as treatment quantities used in this experiment were initially based on concentrations in past literature. Analysis showed the following N concentrations were added: 19.5 g N m^{-2} commercial fertilizer, 18.5 g N m^{-2} forest soil, 12.0 g N m^{-2} *Cecropia*, 10.5 g N m^{-2} *Cyathea*.

The mostly bare portions of the five chosen landslides were cleared of remaining vegetation in a 3×6 m^{2} area in the upper half of each landslide. The lower-half of each landslide, or deposition zone, was avoided because biotic (e.g., organic matter of both living and non-living material) and abiotic (e.g., slope, soil nutrients) conditions are different from the majority of the landslide area (Guariguata 1990). Seventy-five plots were established on each landslide (60 plots of 10×20 cm^{2} used for seed and seedling sampling; 15 plots of 20×20 cm^{2} used for soil sampling). Soil treatments (*Cecropia, Cyathea*, forest soil, fertilizer, control) were randomly assigned to each plot. Soil to 10 cm depth was excavated at each plot, mixed with the respective treatment, and replaced into the excavated hole. A buffer distance of at least 10–20 cm was established between each plot, and aluminum barriers were added to 6 cm depth to restrict soil mixing and treatment loss from overland flow but permit leaching. For the control soil treatments, existing soil was only mixed to 10 cm depth and replaced *in situ*. In total, 225 small plots were arranged over the five sites (five landslides × five soil treatments × three seed treatments × three replicates) and 75 large plots were arranged over the sites (five landslides × five soil treatments × three replicates) in June 2000. Two soil samples (1.9 cm diameter corer to 10 cm depth) were pooled from each large plot just prior to treatment addition. This initial soil sampling provided baseline (pre-treatment) soil data that was used to subtract from subsequent soil samplings. This was done in order to account for spatial variation within the landslide. Soil was then sampled (post-treatment) at 60, 210 and 370 days, and analyzed for gravimetric soil moisture (% of dry mass), soil organic matter (SOM; % loss on ignition), pH (1:1 paste of soil and de-ionized water), total N and P (Kjeldahl digestion followed by colorimetric analysis; Alpkem Corporation 1992), and available P (Bray-1 test; Kuo 1996). Available N (NH_4^+ and NO_3^-) and mineralizable N was determined on field moist soils extracted with 2 M KCl sampled after 45 and 360 days, followed by 14 days field incubations (Binkley and Vitousek 1989). There was not a pre-treatment sampling for available N or N mineralization.

A screen-house experiment was set up at El Verde Field Station (350 m a.s.l.) on two 1.2×3.2 m^2 benches, placed in the middle of a forest gap to mimic high-light conditions characteristic of recent landslides (Table 1). Fiberglass mesh screening (1×2 mm^2 mesh) was used to cover the side-walls and top of the bench to keep out litterfall and most seeds, while creating minimal shading (1110 μ Einsteins m^{-2} s^{-1} inside vs. 1800 μ Einsteins m^{-2} s^{-1} outside the screen-house on a cloudless day with Li-Cor quantum photometer model LI-185B). Identical treatments as used in the field experiment were randomly assigned to 120 small (10×20 cm^2) aluminum trays (five soil treatments × three seed treatments × eight replicates) and mixed with recent volcaniclastic landslide soil in the same concentrations as used in the field experiment. Each tray was perforated at the bottom to allow drainage. Treatments were begun in July 2000 and soils were sampled a year later from controls to 5 cm depth in trays with no seed additions, then analyzed following the methods described for the landslide soils in the field experiment. Available soil N was not determined for screen-house soils.

Plants

Seeds of the herbaceous *Phytolacca rivinoides* Kunth and Bouché (Phytolaccaceae) and the perennial grass *Paspalum millegrana* Schrad. (Poaceae) were chosen as bioassays to test soil treatment effects (*Cecropia, Cyathea*, forest soil, fertilizer, control) on germination, seedling establishment, and seedling growth. Both plant species are common landslide colonists. In June 2000, 100 seeds of each species (from pooled local collections from >5 individuals) were sown on the soil surface of 30 small plots (15 plots for each seed species) on each landslide. Seed germination was monitored on each landslide every 4–6 days, between 27 June and 12 August 2000, and new germinants were removed. Germination was reported as percent of viable seeds sown. Thirty seeds were sown in October 2000 into each of the same plots (following removal of pre-existing seedlings) in order to measure seedling establishment and growth. Eighty days after sowing, seedlings were thinned at random to a maximum of six individuals per plot, marked, and measured for height (cm) from the soil–shoot interface to the tallest foliar structure. After 235 days, percent survival of seedlings since the January 2001 thinning was calculated, as well as seedling height, and total biomass.

An identical experiment was conducted in the screen-house except that seed germination was not monitored, and following thinning to six seedlings after 80 days, three seedlings were harvested after 160 days, and the final harvest was after 245 days.

Statistical analysis

A combination of multivariate-, two-way, and one-way analysis of variance (ANOVA) was performed on the data after checking variables for normal distribution and equal variance. All analyses used General Linear Models procedures of SAS (SAS Institute 1996), and mixed-models were used when sites (landslides) were compared (random effect) in addition to treatments (fixed effects). Repeated measures MANOVAs were used when comparing time periods, and whenever possible all related variables were put into a single MANOVA model (von Ende 1993). Pre-treatment field measurements (before amendments) were subtracted from all subsequent field-sampling periods for SOM, total N, total P, available P, pH, and soil moisture prior to analysis in order to account for within landslide variability. Because of the high mortality of *Phytolacca* seedlings in the field experiment, biomass, height, and survival were not statistically analyzed. Seedling survival for *Paspalum* was arcsin square-root transformed before analysis.

For all analyses, significant ($p \leq 0.05$; Wilks' Lamda) multivariate comparisons were followed by examination of two-way ANOVAs, or one-way ANOVAs of each variable within each sampling period to identify the variables contributing to the significant multivariate response. Type III effect sums of squares were used for all parametric tests in order to adjust for all effects and interactions (SAS Institute 1996). Tukey's post hoc test (Steel and Torrie 1980; Milliken and Johnson 1992) was also performed when a significant ($p < 0.05$) F value was found. 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 treatment effects and significant time × treatment interactions were the focus of this study.

Results

Soils

Landslides in the LEF result in highly variable soil conditions, as shown by the pre-treatment soil variables (i.e., SOM, total N, total P, available P, pH, moisture; Table 2). Following soil treatments in the field, and therefore subtraction of all pre-treatment soil values (Table 2) from the post-treatment soil values, there were significant treatment responses during individual sampling periods (Table 3a). Overall, fertilizer, forest soil, and *Cecropia* accounted for the majority of the differences in soil responses to treatments, whereas *Cyathea* did not alter any of the soil properties (Table 4). The time since soil treatment was important to all landslide sites (Table 3a), as the number of treatment effects declined with time (Table 4). Despite the high landslide variability, significant site × treatment interactions were not present for any of the individual soil variables over the course of the study (Table 3a). Therefore, treatment responses, when present, were consistent across all landslides.

The change from pre-treatment soils by the addition of forest soil caused significantly higher SOM ($p = 0.04$) and higher total N ($p = 0.03$) in the field experiment when compared to the control plots 60 days after soil treatment (Table 4). After 210 days, SOM was significantly higher in the *Cecropia* treatment than in the control ($p = 0.04$; Table 4). Only fertilized soils had significantly higher available P than the control after 60 days ($p = 0.003$; Table 4). Despite no treatment differences after 60 days, total P in the control treatment was significantly higher than *Cecropia* 210 days after soil treatment addition ($p = 0.04$), and total P levels were not significantly different among treatments during other time periods (Table 4).

Soil pH (difference from pre-treatment 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 days sampling periods and then increased. Fertilizer caused soil pH to drop significantly lower than all other soil treatments after 60 days ($p < 0.0001$; Table 4). At 210 days, pH of fertilizer and forest soils were significantly lower than *Cecropia* ($p = 0.004$), and after 370 days forest soil was significantly lower than *Cecropia* ($p = 0.04$;

Table 2. Pre-treatment soil chemical and physical properties for each of the five landslides used in the field experiment in the Luquillo Experimental Forest, northeastern Puerto Rico.

Landslide	SOM (% dry mass)	Total N (μg N g soil^{-1})	Total P (μg P g soil^{-1})	Avail P (μg P g soil^{-1})	pH	Moisture (% dry mass)
ES5	11.81 ± 0.09	123.35 ± 28.25	349.60 ± 19.72	0.57 ± 0.07	5.36 ± 0.06	65.33 ± 1.03
ES10	15.92 ± 0.55	277.66 ± 32.76	382.80 ± 37.18	0.84 ± 0.34	4.44 ± 0.04	33.76 ± 1.95
J4	14.88 ± 0.22	161.44 ± 22.60	183.52 ± 10.02	0.61 ± 0.15	4.82 ± 0.04	51.29 ± 1.48
RB10	6.15 ± 0.19	172.60 ± 14.38	135.19 ± 12.57	6.55 ± 0.41	5.05 ± 0.02	33.51 ± 0.92
MY8	7.88 ± 0.20	87.5 ± 16.0	222.93 ± 9.89	1.89 ± 0.22	4.94 ± 0.01	41.94 ± 1.05

All soils were sampled 0–10 cm depth (mean ± SE; $n = 15$) immediately prior to treatment additions in June, 2000.

Table 3. Summary table of repeated-measures MANOVA for (a) the six field soil variables (subtracted from pre-treatment values): SOM, total N, available P, total P, moisture, and pH where the measurements were at 60, 210, and 370 days, and (b) the three field-available soil nitrogen variables:NH_4^+,NO_3^-, N-mineralization where the measurements were at 45 and 360 days.

Source	Num d.f.	Den. d.f.	*p*
(a) SOM, total N, total P, available P, pH, moisture			
Between subjects			
Site	4	50	0.1910
Treatment	4	50	0.3294
Site*Treatment	16	50	0.8302
Within Subjects			
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
(b) NH_4^+,NO_3^-, N-mineralization			
Between subjects			
Site	4	43	0.0049
Treatment	4	43	< 0.0001
Site*Treatment	16	43	0.0026
Within subjects			
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

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.

Table 4). Soil moisture (difference from pre-treatment) was not significantly different among treatments for any of the sampling periods ($p > 0.05$). Similarly, soil bulk density, measured only at 370 days after treatment addition, was not significantly different among soil treatments ($p > 0.05$).

Soil NH_4^+, NO_3^-, N-mineralization were not sampled pre-treatment, and therefore the means were not adjusted to account for within landslide variability. Furthermore, responses to treatments were slightly more complex for available N soil variables (NH_4^+, NO_3^-, N-mineralization) than for the other field soil variables described above, as site, treatment, and site × treatment interactions were significant when available N soil variables were averaged across the two sampling periods (between-subjects; Table 3b). However, the addition of fertilizer was the only treatment that altered available N and N-mineralization in this study, as NH_4^+ ($p = 0.0002$), NO_3^- ($p < 0.0001$), and N-mineralization rates ($p = 0.0002$) were higher than all other soil treatments at the 45 days sampling period (Table 5). Therefore, the available N changes resulting from fertilizer addition were immediate and short-lived, as there were no treatment effects for available N or N-mineralization among any of the treatments at 360 days (Table 5).

Soil treatment differences were also apparent in the screen-house experiment (Num. d.f. = 24, Den d.f. = 106, $p < 0.0001$), and followed some of the same patterns as the field experiment. 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 ($p < 0.0001$; Figure 1). 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 ($p < 0.0001$; Figure 1). Neither total soil P nor available 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 ($p < 0.0001$; Figure 1). Soil moisture was significantly higher in *Cyathea* when compared to fertilizer ($p = 0.02$; Figure 1).

Table 4 A comparison of treatment effects for the following soil parameters measured on five landslides in the LEF, Puerto Rico: SOM (%), total N (μg N g soil^{-1}), total P (μg P g soil^{-1}), available P (μg P g soil^{-1}) pH (log scale), moisture (% dry mass).

	SOM	Total N	Total P	Avail P	pH
60 days					
Treatment					
Cecropia	0.65 ± 0.20^{ab}	181.19 ± 43.23^{ab}	31.40 ± 20.40	-0.02 ± 0.31^{a}	0.02 ± 0.05^{a}
Cyathea	0.47 ± 0.15^{ab}	108.93 ± 37.50^{ab}	36.06 ± 19.72	0.41 ± 0.18^{ab}	-0.02 ± 0.05^{a}
Forest soil	0.75 ± 0.14^{a}	205.62 ± 41.77^{a}	-22.12 ± 27.52	-0.13 ± 0.25^{a}	-0.12 ± 0.04^{a}
Fertilizer	0.30 ± 0.14^{ab}	104.70 ± 34.43^{ab}	23.60 ± 20.52	1.59 ± 0.62^{b}	-0.30 ± 0.05^{b}
Control	0.14 ± 0.14^{b}	53.28 ± 38.82^{b}	44.85 ± 21.00	-0.26 ± 0.19^{a}	-0.06 ± 0.05^{a}
210 days					
Treatment					
Cecropia	0.84 ± 0.22^{a}	143.12 ± 38.15	21.72 ± 16.08^{a}	-0.05 ± 0.25	-0.16 ± 0.06^{a}
Cyathea	0.47 ± 0.18^{ab}	95.34 ± 31.49	40.59 ± 22.17^{ab}	0.16 ± 0.25	-0.26 ± 0.04^{ab}
Forest soil	0.74 ± 0.13^{ab}	209.45 ± 37.14	31.79 ± 21.58^{ab}	0.0001 ± 0.31	-0.34 ± 0.04^{ab}
Fertilizer	0.37 ± 0.18^{ab}	107.45 ± 36.89	41.97 ± 22.71^{ab}	0.60 ± 0.40	-0.36 ± 0.07^{b}
Control	0.31 ± 0.13^{b}	138.57 ± 71.27	129.86 ± 41.89^{b}	-0.14 ± 0.22	-0.25 ± 0.03^{b}
370 days					
Treatment					
Cecropia	0.65 ± 0.25	209.79 ± 43.23	7.11 ± 17.30	0.95 ± 1.74	0.02 ± 0.04^{a}
Cyathea	0.66 ± 0.19	145.35 ± 36.97	26.58 ± 21.18	0.14 ± 0.40	-0.08 ± 0.04^{ab}
Forest soil	0.57 ± 0.13	292.15 ± 76.28	12.73 ± 25.31	-0.17 ± 0.32	-0.12 ± 0.03^{b}
Fertilizer	0.40 ± 0.17	153.42 ± 46.40	42.43 ± 23.09	0.02 ± 0.40	-0.09 ± 0.03^{ab}
Control	0.05 ± 0.22	111.89 ± 49.57	15.72 ± 25.86	-0.07 ± 0.42	-0.07 ± 0.03^{ab}

Results are based on differences from pre-treatment means (see Table 2) at the various sampling periods (60, 210, 370 days) following soil treatments. Values followed by letters indicate the presence of a significant difference between unlike letters in a given column and sampling period. Soil moisture did not significantly differ among treatments at any of the sampling periods.

Plants

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 (Figure 2). 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 twofold 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 days after seed sowing. Moreover, *Paspalum* seedling biomass was not different among soil treatments 235 days after sowing ($p > 0.05$), though seedlings in fertilizer tended to have the highest biomass (fertilizer 556.5 ± 247.5; forest soil 260.2 ± 110.4; control 176.7 ± 79.1; *Cecropia* 140.2 ± 63.1; *Cyathea* 133.4 ± 35.2 mg). There were too few *Phytolacca* seedling survivors at 235 days to analyze statistically.

In the screen-house experiment, seedling biomass and height for both *Paspalum* ($p < 0.0001$) and *Phytolacca* ($p < 0.0001$) significantly differed among soil treatments when averaged across sampling periods as well as for each individual sampling period. Fertilizer, followed by forest soil, had significantly higher *Paspalum* seedling biomass during all three sampling periods ($p < 0.0001$; Figure 3a), and there were no significant biomass differences among *Cecropia, Cyathea*, and control treatments ($p > 0.05$; Figure 3a). Similar results were found for *Phytolacca* seedling biomass (Figure 3b). However, for *Phytolacca* seedlings, there were too few survivors in the *Cecropia, Cyathea*, and control treatments for analysis at 245 days. Seedling heights followed similar overall patterns as biomass for*Paspalum* ($p < 0.0001$) and *Phytolacca* ($p < 0.0001$), with the exception that *Paspalum* seedlings were significantly shorter in *Cecropia* and *Cyathea* treatments when compared to the control after 80 and 160 days following soil treatment (data not shown).

Seedling survivorship at 160 days was high for both *Paspalum* (100 ± 0.00%) and *Phytolacca*

Table 5. Soil NH_4^+ and NO_3^- concentrations (μg g soil^{-1}) and soil N-mineralization (μg g soil^{-1} day^{-1}) 45 and 360 days following soil treatments (mean ± SE).

	45 days			360 days		
	NH_4^+	NO_3^-	N-mineralization	NH_4^+	NO_3^-	N-mineralization
Treatment						
Cecropia	0.03 ± 0.01^a	1.02 ± 0.33^a	0.53 ± 0.10^a	7.62 ± 4.09	2.28 ± 0.53	0.56 ± 0.22
Cyathea	0.07 ± 0.04^a	1.77 ± 0.45^a	0.66 ± 0.21^a	3.37 ± 0.59	2.85 ± 1.00	0.20 ± 0.10
Forest soil	0.19 ± 0.07^a	4.29 ± 1.18^a	0.70 ± 0.19^a	3.90 ± 0.59	2.22 ± 0.83	0.15 ± 0.11
Fertilizer	0.89 ± 0.31^b	26.06 ± 5.24^b	4.55 ± 1.87^b	3.62 ± 0.55	3.15 ± 0.92	0.09 ± 0.10
Control	0.12 ± 0.05^a	2.04 ± 0.68^a	0.42 ± 0.08^a	2.95 ± 0.32	3.31 ± 1.07	0.16 ± 0.09

Treatment means are from five landslides in the LEF, Puerto Rico. Different letters within columns during the 45 days sampling indicate significant differences between treatments. There were no significantly different nitrogen concentrations among treatments at 360 days.

Table 6. Mean (±SE) percent surviving seedlings following additions of the five soil treatments used in the field experiment (235 days following seed sowing; 370 days following soil treatments), and the screen-house experiment (245 days following seed sowing and soil treatments; at El Verde Field Station) in the LEF, Puerto Rico.

	Field		Screen-house	
	Paspalum	*Phytolacca*	*Paspalum*	*Phytolacca*
Treatment				
Cecropia	95.82 ± 2.87^{ab}	7.14 ± 7.14	49.95 ± 8.90^a	0.00 ± 0.00
Cyathea	97.43 ± 2.57^a	0.00 ± 0.00	45.80 ± 12.50^a	0.00 ± 0.00
Forest soil	95.23 ± 2.73^{ab}	12.48 ± 8.24	95.82 ± 4.20^b	45.80 ± 12.50^a
Fertilizer	97.17 ± 1.92^{ab}	18.75 ± 11.15	87.50 ± 12.50^b	79.14 ± 8.78^a
Control	84.62 ± 10.42^b	0.00 ± 0.00	33.30 ± 8.90^a	0.00 ± 0.00

Different letters in columns indicate significant differences among treatments. *Phytolacca* did not have enough surviving individuals to compare statistically in the field experiment.

(90.41 ± 4.79%) in the screen-house experiment and there were no significant differences among treatments for either seedling species. Survival of *Paspalum* seedlings at 235 days (370 days since soil treatment) was > 80% for all treatments in the field, but lower under the more controlled conditions of the screen-house at 245 days (Table 6). In the field, *Paspalum* seedlings in *Cyathea*-treated soil had significantly greater survival than those sown in controls ($p = 0.01$; Table 6), and *Paspalum* in forest soil and fertilizer treatments had greater survival than all other treatments in the screen-house ($p < 0.0001$). *Phytolacca* did not survive as well as *Paspalum* in the field or in the screen-house, and both experiments resulted in the absence of *Phytolacca* survivors in *Cyathea*-treated soils and in the control treatments at 245 days (Table 6). *Cecropia*-treated soil only had one *Phytolacca* survivor in the field (Table 6). Although fertilized soils tended to have a higher percentage of surviving *Phytolacca* seedlings compared to forest-amended soils after 245 days, 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 days (Table 6).

Discussion

Soils

Each of three additions of common types of organic matter to landslides in the Luquillo Experimental Forest (LEF; *Cecropia* and *Cyathea* leaves and forest soil) had a unique effect on landslide soils but that effect was consistent across heterogeneous landslides. For example, forest soil additions provided immediate increases in SOM and total N that, like the effects of fertilizer additions on available N and P, declined after 60 days. In contrast, *Cecropia* leaves increased SOM only after 210 days and *Cyathea* leaves had no effect on landslide soils except in the

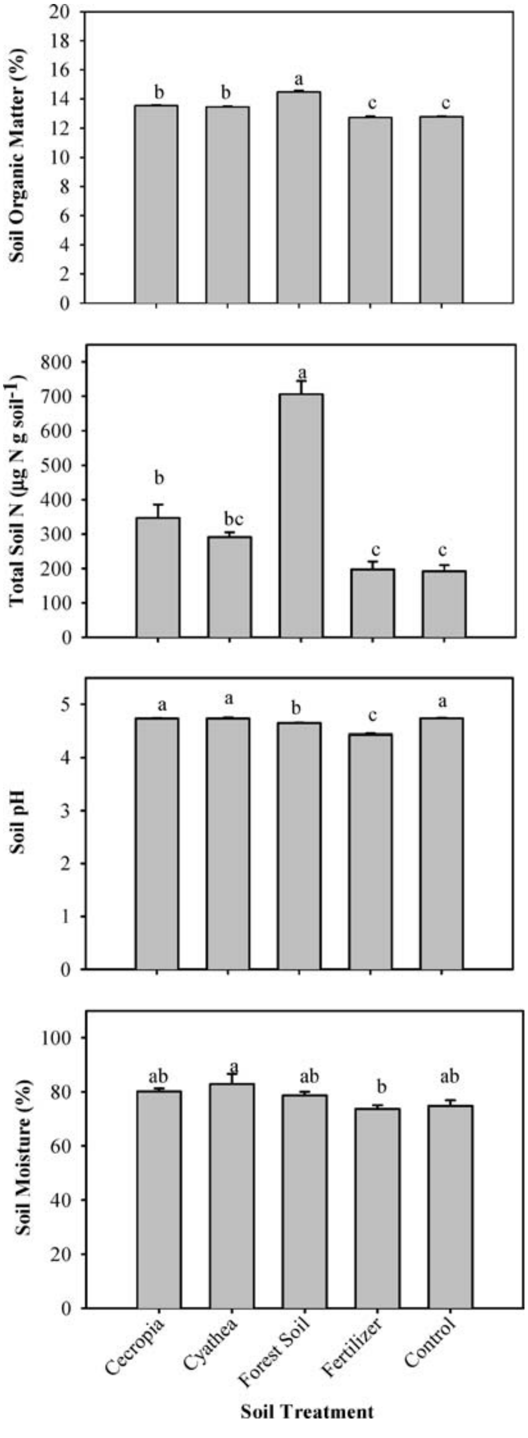

Figure 1. Mean (±SE) for respective soil variables sampled (0–5 cm depth) in the screen-house experiment at El Verde Field Station, Puerto Rico. Sampling took place in July 2001, which was one year following soil treatment additions to landslide soil. Different letters indicate significant treatment differences.

screen-house experiment. Alleviating the severe, nutrient-poor conditions common to landslides is critical for plant succession (Fetcher et al. 1996; Walker et al. 1996) and development of ecosystem structure (Silver et al. 1996), especially in tropical rainforests where nutrients are quickly leached or recycled by the biota (Lodge et al. 1994). The variable impacts of common organic matter inputs is therefore instrumental in creating and maintaining resource patchiness in early primary succession on Puerto Rican landslides.

Resource patchiness within a landslide is highly dynamic, both spatially and temporally. After the initial increase associated with fertilizer and forest soil patches on landslides, soil fertility declined, resulting from nutrient loss from leaching, sorption, and/or biotic uptake. Leaves of *Cecropia* and *Cyathea* had minimal positive effects on soil fertility within a year because release of nutrients into the landslide soil depends on the processes of decomposition. *Cecropia* decomposes more slowly and retains more N than *Cyathea* on these same landslides (Shiels in press), which further contributes to the variable soil patchiness revealed by the addition of these two leaf species to landslide soil. Additions of carbon substrates to soil does not always produce positive soil effects, as immobilization of nutrients, such as N, contribute to the dynamics of soil nutrient patchiness, as found in a previous LEF study (Zimmerman et al. 1995) and in other studies in temperate systems (Zink and Allen 1998; Reever Morghan and Seastedt 1999). Although significant microbial immobilization was not found in this study, *Cecropia* and *Cyathea* treatments tended to have NH_4^+ and NO_3^- averages slightly lower than controls when compared at the 45 days time period, and some microbial immobilization of P could have also accounted for the surprising increase in total soil P in the control when compared to *Cecropia*-treated soil. Despite the minimal treatment effects for these leaves in the field, the higher SOM for both leaf types and higher total N for *Cecropia* in the screen-house suggest that more stable field conditions or longer-term incorporation and decomposition of leaf litter may produce some benefit of leaves to soil fertility in landslides. The timeframe for such potential changes is unclear, as nutrient availability from decomposing leaves will depend on site conditions (e.g., microclimate, soil nutrition; Swift et al. 1979), the presence of decomposers, such as

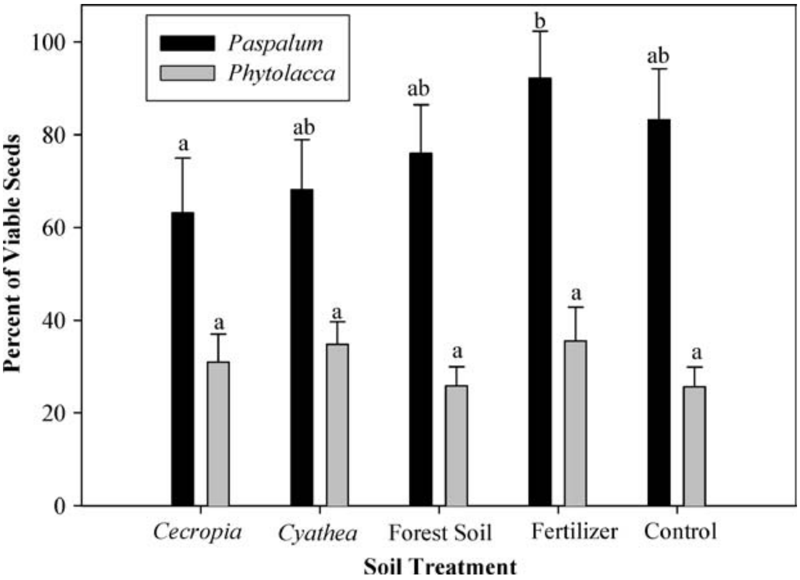

Figure 2. Mean (±SE) percent seed germination (% of viable seeds) of *Phytolacca* and *Paspalum* sown in the five soil treatments on five landslides in the LEF, Puerto Rico. Different letters for respective seed types indicate significant differences among soil treatments over the 45 days experiment.

microbial communities, which are few or absent on recent landslides (Calderon-González 1993; Shiels and Yang unpublished data; D.J. Lodge pers. commun.), and the chemical composition of the leaves (Melillo et al. 1982; Palm and Sanchez 1991; Shiels in press). We show that forest soil provided more available organic matter and nutrients than leaf litter, but all three types of organic matter additions may alleviate the extreme soil infertility on landslides over longer time periods.

Forest soil and *Cecropia* leaf additions to landslides had the longest lasting effects on soil because they significantly altered soil pH at 210 and 370 days. Although soil pH directly affects soil microorganisms and the availability of plant nutrients (Sparks 1995; Sollins 1998), clear correlations between pH and nutrient availability were not present in this study or in another landslide study in the LEF that measured soil microorganisms, pH, and soil carbon (Li et al. 2005). The fluctuation and lowering of pH after treatment addition shown in this study can be attributed to a combination of seasonality and soil disturbance (Silver et al. 1996; Sollins 1998) resulting from the physical mixing of the soils *in situ* (Foth and Ellis 1997) as well as addition of organic matter (Jenny 1980; McLean 1982; Sparks 1995) and NH_4^+-based fertilizer (Sparks 1995; Foth and Ellis 1997). Although the tropical soils in the LEF are highly weathered and have relatively low pH values that may be lowered further with organic matter inputs, the lasting effects of decreased soil pH do not overwhelm the increased soil fertility from forest soil additions.

Plants

Linking soil resource patchiness and plant development in LEF landslides can be accomplished by measuring vegetation responses to the organic matter and nutrient treatments. Availability of nutrient resources on landslides varies with time and space (Guariguata 1990; Shiels 2002); therefore, vegetation development on landslides should also depend on the timing of establishment in areas of higher nutrient sources. We show that the presence of nutrient availability (inorganic nutrients or forest soil) when seeds and seedlings are present in landslide soils will produce increased plant growth and survival.

Seed germination is influenced by soil patches of higher inorganic nutrients for the landslide-colonizing species *Paspalum millegrana*, as this grass

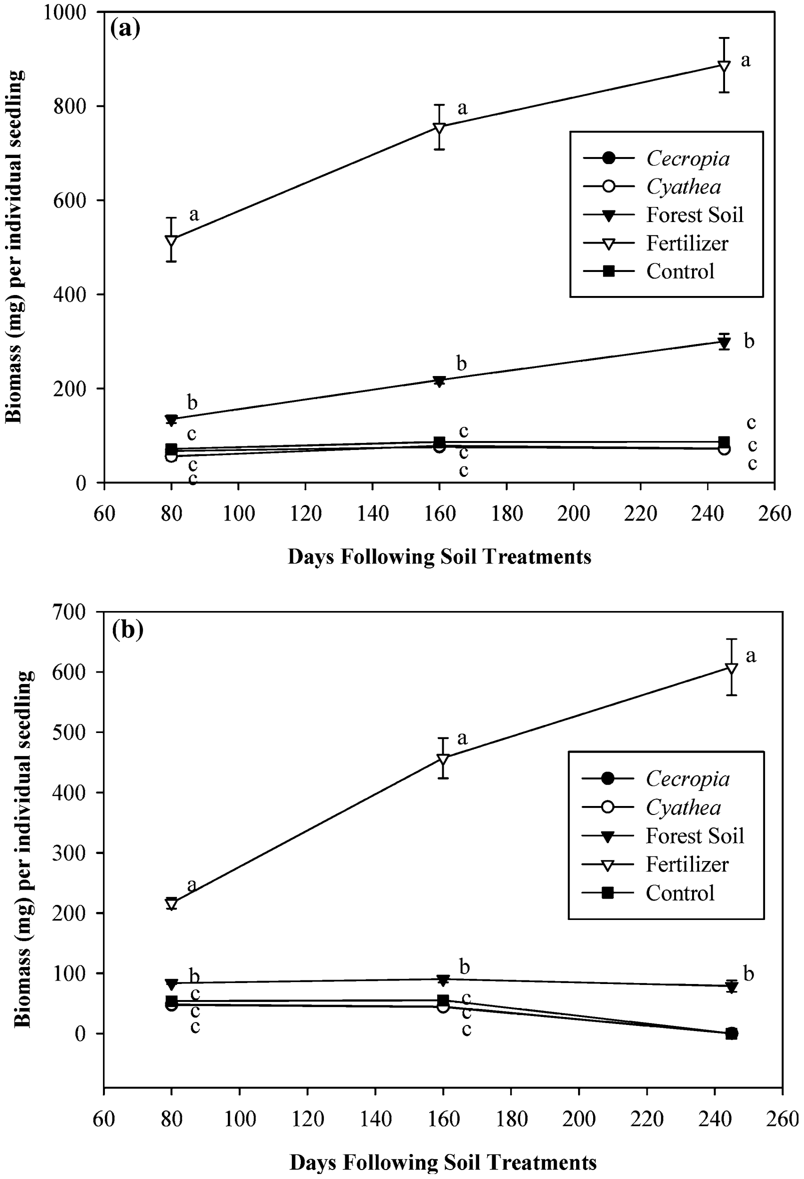

Figure 3. Mean (±SE) (a) *Paspalum* biomass (mg indiv.$^{-1}$), and (b) *Phytolacca* biomass, (mg indiv.$^{-1}$) measured during 80, 160, and 245 days after soil treatment additions to the screen-house experiment. Different letters during each respective time period indicate significant differences among treatments for each seedling species. *Phytolacca* seedlings in *Cecropia, Cyathea*, and Control treatments were not present during the 245 days sampling. Therefore, analysis was not conducted on these soil treatments.

responded to the commercial fertilizer treatment in the field by exhibiting higher germination than in *Cecropia*-treated soil across all landslides. This finding reflects the results of the soil nutrient analyses in the field experiment, and also supports the possibility of nutrient immobilization in *Cecropia*- and *Cyathea*-treated soils (as noted above). Therefore, seed germination of *Paspalum* may be influenced positively by soils with higher soil fertility and negatively by the existence of leaf litter, like *Cecropia*, incorporated into the landslide soil. 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-month-old landslide in the LEF (L. Walker personal observation). However, the successful germination of *Paspalum* (77%) and *Phytolacca* (31%) in the harsh environment of landslides (Fernández and Myster 1995) indicates that germination may not be as limiting to plant colonization and vegetation development on Puerto Rican landslides as other characteristics, such as seed arrival (Shiels and Walker 2003) and nutrient availability (Walker et al. 1996; this study).

Growth of *Pasplum* and *Phytolacca* seedlings did not vary by treatment in the field, perhaps due to the rapid loss of treatment effects on soil fertility prior to seed sowing. As shown in the soil analyses, if nutrients are not utilized quickly, they are lost from the top 10 cm of soil. *Phytolacca* seedlings had higher biomass in the forest soil and fertilizer treatments when compared to all other treatments in the screen-house, and only survived in forest soil and fertilizer treatments (with the exception of one survivor in *Cecropia*-treated soil) in both the screen-house and the field, indicating that colonization and survival of this species in landslide soil is optimized by establishing in higher nutrient patches. *Paspalum* seedlings survived longer (> 235 days) than *Phytolacca* seedlings in landslide soil regardless of treatment, and had higher biomass in the forest soil and fertilizer treatments when compared to all other treatments in the screen-house. The presence of this same growth response for both seedlings supports conclusions of past studies, both in the LEF (Guariguata 1990; Fetcher et al. 1996) and in Jamaica (Dalling and Tanner 1995) that nutrients are limiting to plant growth in landslide soils. Additionally, with high inputs of seed rain (Shiels and Walker 2003), high germination success, and extended survival, even in unfertilized soils, *Paspalum* is likely to colonize landslides quickly and survive for extended periods of time, which 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 and Boneta 1995; Walker et al. 1996) and in Hawaii (Restrepo and Vitousek 2001).

Organic matter does not positively influence plant growth on LEF landslides unless it is in the form of forest soil. The facilitative effects of forest soil on seedling growth found here reflect the importance of patches of forest soil on landslides providing more suitable sites for plant growth and landslide succession. While some soil properties were elevated in the screen-house for *Cecropia* and *Cyathea* leaf litter additions (e.g., SOM, total N), and in one case in the field experiment (SOM in *Cecropia*-treated soil), plant establishment and growth did not increase with the addition of either of these two treatments. In a world-wide study of the effects of leaf litter on vegetation, Xiong and Nilsson (1999) demonstrated that plant litter generally has a negative effect on seed germination, establishment, and aboveground biomass. Interestingly, in the screen-house experiment, *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. While leaf litter did not always produce negative effects when mixed into landslide soil, it did not facilitate germination, survival, or plant growth. Therefore, previous predictions that organic matter in general is necessary for plant colonization on landslides may be misleading. Instead, on LEF landslides, the type of organic matter substrate, the frequency with which it is deposited into recent landslides, and the presence or absence of biota directly influence soil nutrient patch dynamics, and these soil conditions will ultimately affect plant development.

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