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ORIGINAL PAPER

Soil factors predict initial plant colonization on Puerto Rican landslides

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Abstract Tropical storms are the principal cause of landslides in montane rainforests, such as the Luquillo Experimental Forest (LEF) of Puerto Rico. A storm in 2003 caused 30 new landslides in the LEF that we used to examine prior hypotheses that slope stability and organically enriched soils are prerequisites for plant colonization. We measured slope stability and litterfall 8–13 months following landslide formation. At 13 months we also measured microtopography, soil characteristics (organic matter, particle size, total nitrogen, and water-holding capacity), elevation, distance to forest edge, and canopy cover. When all landslides were analyzed together, plant biomass and cover at 13 months were not correlated with slope stability or organic matter, but instead with soil nitrogen, clay content, water-holding capacity, and elevation. When landslides were analyzed after separating by soil type, the distance from the forest edge and slope stability combined with soil factors (excluding organic matter) predicted initial plant colonization on volcaniclastic landslides, whereas on diorite landslides none of the measured characteristics affected initial plant colonization. The life forms of the colonizing plants reflected these differences in landslide soils, as trees, shrubs, and vines colonized high clay, high nitrogen, and low elevation volcaniclastic soils, whereas herbs were the dominant colonists on high sand, low nitrogen, and high elevation diorite soils. Therefore, the predictability of the initial stage of plant succession on LEF landslides is primarily determined by soil characteristics that are related to soil type.

Keywords Organic matter · Primary succession · Sediment runoff · Soil nitrogen · Soil particle size · Slope stability

Introduction

Landslides are common disturbances in steep, wet environments such as tropical montane rainforests.

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Landslides initiate primary succession and create heterogeneous biotic and abiotic conditions that influence the structure and composition of recovering vegetation on spatial scales ranging from landscapes to microsites (Guariguata 1990; Walker et al. 1996; Vittoz et al. 2001; Shiels et al. 2006). The initial conditions of a successional sere directly affect the pathways of vegetation and soil development (Walker and Chapin 1987; Tagawa 1992; Eriksson and Eriksson 1998; Walker and del Moral 2003). Therefore, an understanding of the environmental characteristics immediately following landslide formation may help to predict succession.

There have been several studies of plant colonization on landslides in the Luquillo Experimental Forest (LEF) in Puerto Rico (Guariguata 1990; Walker 1994; Zarin and Johnson 1995a, b; Fetcher et al. 1996; Walker et al. 1996; Shiels et al. 2006). However, the specific factors that control plant colonization on landslides within the LEF remain uncertain. Walker et al. (1996) proposed that hill slope stability and the presence of organic matter are two of the most critical factors controlling plant colonization on Caribbean landslides. Guariguata (1990) demonstrated that plant abundance and basal area were higher in the flatter landslide deposition zone that contained higher soil carbon and soil nutrients compared to the steeper, upper portions of the landslide. Zarin and Johnson (1995a, b) determined that soil development increases with landslide age, and they hypothesized that increased levels of soil organic matter (SOM) determine vegetation recovery on landslides. Despite these findings, a study in Alaska refutes the importance of slope in determining plant colonization and distribution (Lewis 1998), and recent findings by Shiels et al. (2006) show that the specific type of organic matter (forest soil versus leaves) incorporated into landslide soil is more critical for increasing soil fertility and plant growth than the mere presence of organic matter. Alternative factors unrelated to slope stability and organic matter may also determine initial vegetation recovery on landslides, such as the proximity to the intact forest for seed dispersal (Walker and Neris 1993; Shiels and Walker 2003) and the soil and substrate type (Myster et al. 1997). The understanding of initial conditions influencing primary succession on landslides remains unknown and clearly requires further evaluation.

A storm on April 17–19, 2003 in the LEF in northeastern Puerto Rico caused many new road-related landslides and provided an opportunity to directly examine factors that control initial (13 month) plant colonization on a set of even-aged tropical landslides. In this study, we determined whether plant colonization on landslides is controlled by slope stability and SOM (as proposed by Walker et al. (1996)). We also examined the influence of elevation, distance to forest edge, canopy cover, litterfall, microtopography, and additional soil characteristics (particle size, nitrogen, and water-holding capacity) on plant colonization.

Methods

Study site

This study was conducted in the LEF in northeastern Puerto Rico (18°18′ N, 65°50′ W) where mean annual precipitation ranges from 3,000 to 4,000 mm, and mean monthly temperatures range from 21 to 25°C (Brown et al. 1983). The LEF covers roughly 110 km^2 (11,000 ha), ranges in elevation from 150 m to just over 1,000 m, and includes four major vegetation zones occurring along an altitudinal gradient. The tabonuco (*Dacryodes excelsa* Vahl.) forest (subtropical wet forest in Holdridge System; Ewel and Whitmore 1973) dominates below 600 m elevation in the LEF. Above 600 m is a subtropical rain forest characterized by palo colorado (*Cyrilla racemiflora*) trees, while above ca. 750 m a dwarf forest occurs and *Tabebuia rigida* and *Ocotea spathulata* are the dominant trees. Nearly monotypic forest stands of palm (*Prestoea montana*) are interspersed throughout all vegetation types in areas of poorly drained soils (Waide and Lugo 1992). Soils derived from volcaniclastic parent material (Ultisols; Cretaceous tuffaceous sandstone and siltstone weathered from extrusive bedrock; hereafter volcaniclastic soils) dominate throughout the LEF, whereas soils in parts of the upper elevations may be underlain by those derived from quartz-diorite bedrock (Inceptisols; weathered from intrusive bedrock; hereafter diorite soils; Seiders 1971; Larsen et al. 1998).

Study design

Of the 100+ landslides that occurred in the LEF as a result of the April 17–19, 2003 storm event, approximately 69 were road-related (within 200 m of a road; Larsen 1995), and were $\geq$12 m^2 in area and <55° slope (A. Shiels, unpublished data). We randomly chose 30 of those 69 landslides for our study. The landslides ranged in elevation from 152 to 825 m a.s.l. (see Appendix 1), spanned tabonuco, palo colorado, palm, and cloud forest types, and were found on areas underlain by both volcaniclastic (n = 8) and diorite (n = 22) soil types. In October 2003, we randomly located two 1 × 1 m plots within the landslide chute (the central area of highest erosion within a landslide; Guariguata 1990) of each of the 30 landslides. The chute portion of the landslide was selected because it was present on all chosen landslides (often road-related landslides have the lower deposition zone removed in order to clear the roadways), and was not too steep to access (the upper, slip-face zones often have near-vertical slopes). The two plots were placed side-by-side on the slope, 30–100 cm apart with edges perpendicular and parallel to the direction of the slope, and they were at least 1 m (mean ± SE = 2.54 ± 0.21 m) from any forest-landslide edge. Each of the two plots was randomly assigned as either a control or litter removal plot. The control plots were used to evaluate the impact of litterfall collection (see below) on SOM and vegetation parameters. In contrast, inside the litter removal plots on each of the 30 landslides, we measured all the parameters for this study, which included: slope stability and litterfall from December 2003 to May 2004 (8–13 months following landslide formation); and in May 2004, we measured microtopography, soil characteristics (organic matter, particle size, nitrogen, and water-holding capacity), elevation, distance to forest edge, canopy cover (measured with a densiometer), and vegetation colonization (see below).

Measurements of slope stability on each 1 × 1 m litter removal plot included slope, sediment runoff, and soil movement. Sediment runoff was measured at the base of each plot using a 100 cm × 8 cm × 7 cm deep, open-top plastic rain gutter placed perpendicular to the slope and tilted to allow flow into a plastic collection bucket. We removed and obtained wet mass of all sediment from the gutters and buckets every 2 weeks from December 2003 to May 2004 (24 weeks), then determined total sediment dry mass by taking subsamples of the sediment wet mass and calculating wet/dry mass ratios. Soil movement was measured by taking the average accumulation or loss of soil at the base of each of six flags placed along the upper edge of each plot and integrated over the entire 24-week period.

Because microtopography of the soil surface can affect plant colonization, we calculated a roughness index (Saleh 1993) of each litter removal plot during May 2004. We measured the depth to the soil surface from an imaginary horizontal plane placed on the highest emergent point from the plot surface and parallel to the plot slope. Measurements were made every 10 cm along three horizontal transects across each plot (25, 50, and 75 cm from the bottom edge; total = 33 measurements per plot).

Organic matter measurements included litterfall (litter removal plots only) and SOM (both control and litter removal plots). Litterfall was collected from each litter removal plot, rinsed to remove sediment and dried at 45°C before weighing. This process was repeated every 2 weeks from October 2003 to May 2004. Soil organic matter (SOM; % loss on ignition), was determined from three soil cores (1.9 cm diameter and 10 cm deep) taken in May 2004 from random locations within each litter removal and control plot. Soils from these cores from the litter removal plots were also analyzed for particle size (% sand and clay; Sheldrick and Wang 1993) and total nitrogen (Kjeldahl digestion followed by colorimetric analysis; Alpkem 1992). An additional soil core (7 cm diameter to 10 cm depth) was taken from each litter removal plot in May 2004 in order to determine the water-holding capacity of the soil by saturating each soil sample, allowing it to drain for 10 min before weighing, and finally drying (to a constant mass at 105°C) before reweighing each sample.

Plant colonization and early successional development on the 30 landslides were evaluated by measuring vegetation cover and biomass from both control and litter removal plots in May 2004. Plants were divided into six categories (trees plus shrubs, herbs, vines, graminoids, ferns, and bryophytes). Because cover estimates are vertical projections onto the ground surface, values can exceed 100%. All aboveground plant biomass (live or standing dead) was removed from each plot (litter removal and control) and dry mass was determined for the same six plant categories used for vegetation cover. Only plants rooted in the plot were harvested. Belowground biomass (coarse roots only) was also estimated in May 2004 by sampling then pooling two cores in each litter removal and each control plot (7 cm diameter, 16 cm depth, 616 cm^3) and manually separating all roots and fern rhizomes (live or dead) >1 mm diameter before drying them to a constant mass.

Statistical analysis

We analyzed 13 variables that we predicted to be important for initial plant colonization. Because there were high levels of collinearity among the predictor variables and the plant colonization variables (35 of 153 possible pairwise correlations among all the variables), we used principal components analysis (PCA) to reduce the number of variables to a smaller number of principal components (PCs) that are orthogonal (i.e., not correlated; Quinn and Keough 2002). Variables entered (with appropriate transformations) into the PCA were slope, elevation, distance to forest edge (log), canopy cover, litterfall (sqrt), microtopography index, soil movement (inverse), sediment runoff (log), soil water-holding capacity (sqrt), SOM, sand, clay, and total soil nitrogen (sqrt). Although we suspected litter removal might influence plant colonization and SOM, *t*-test analyses between the control and litter removal plots revealed no significant differences ($P > 0.05$) for these measurements. Because we only measured all of the relevant variables on the litter removal plots, we only used the litter removal plots for PCA and predicting plant colonization. Following PCA, we interpreted the identity of the PCs based on the recommendations of Comrey (1973; cited in Tabachnick and Fidell 1996) who found that a factor-loading of 0.63 represents 40% overlapping variance between the variable and the PC. Thus we used factor-loadings of 0.63 and higher when assigning significance to a particular variable within a PC. We then used the PCs to calculate factor scores for each landslide and used these factor scores in multiple regressions to test whether the PCs (linear combinations of the variables weighted by the contributions to the PCs) are correlated with the following variables related to plant succession: vegetation cover, aboveground biomass, belowground biomass, and total biomass.

The initial analysis strongly indicated that soil type was a primary factor in explaining mountain-wide variation; therefore we conducted two additional PCAs for volcaniclastic and diorite landslides that were necessary for uncovering factors affecting plant colonization on a subset of LEF landslides distinguished by underlying soil type. All linear regressions were considered significant if $P < 0.05$. Means of soil and vegetation parameters from the volcaniclastic and diorite soil types were also compared with MANOVA and *t*-tests. We conducted PCA analyses using Statistica (StatSoft Inc. 2002) while other tests were performed using SPSS (SPSS 1998).

Results

For all 30 landslides combined, the pattern of succession was affected by some soil characteristics (particle size, total nitrogen, and water-holding capacity) and elevation, but not by other soil characteristics (stability, organic matter) or litterfall. The first four PCs accounted for 68.98% of the variation in the entire data set (Table 1). Principal component 1 was dominated by variables related to soil characteristics of the landslides (excluding SOM), and elevation (Table 1). Elevation largely distinguishes the two dominant soil types (volcaniclastic and diorite) in the LEF, and measured variables reflect this difference between the two soil types (Table 2). Principal component 2 was dominated by the distance to the forest edge (Table 1), and the dominant variable in PC 3 (soil movement) is an indicator of slope stability. Principal component 4 did not have any variables above the 0.63 factor-loading cutoff. We examined the relationship of the PCs for the different soil types as a way of verifying that the PCs were allowing us to discriminate among an independent variable not included in the analysis (i.e., soil type). Diorite and volcaniclastic landslides were well separated by variation along PC 1 (Fig. 1). Two volcaniclastic landslides were at high elevation (815 and 825 m a.s.l.), and one of these had PC values resembling the diorite landslides (Fig. 1).

Principal Component 1 for the 30 landslides was significantly positively correlated with vegetation

Table 1 Eigenvalues and factor-loadings for the first four principal components of variables measured after disturbance from 30 landslides in the Luquillo Experimental Forest, Puerto Rico

Variable[a]	PC 1	PC 2	PC 3	PC 4
Eigenvalue	4.20	1.78	1.57	1.42
% of total variance explained	32.29	13.72	12.08	10.89
Slope	−0.571	0.182	0.009	0.585
Elevation	**−0.777**	0.003	−0.281	−0.188
Distance to forest edge	0.140	**0.633**	0.083	−0.232
Average % canopy cover	0.400	−0.553	−0.446	0.306
Average litterfall	0.590	−0.565	−0.057	0.247
Microtopography index	0.101	−0.578	−0.205	−0.205
Average soil movement	−0.168	0.188	**−0.780**	−0.409
Average sediment runoff	−0.220	−0.376	0.396	−0.621
Soil organic matter	0.281	0.248	−0.499	0.277
% sand	**−0.867**	−0.246	0.131	0.034
% clay	**0.907**	0.283	0.060	−0.016
Total nitrogen	**0.738**	0.097	0.369	0.001
Soil water-holding capacity[b]	**0.674**	−0.046	−0.260	−0.396

[a] The factor-loading cutoff (0.63) was based on the findings of Comrey (1973), and each variable equal to or exceeding that cutoff is shown here in bold

[b] Soil collections were from 0 to 10 cm depth

Table 2 Soil properties (0–10 cm depth), sediment runoff, and litterfall (mean ± SE) on 13-month-old landslides with two different soil types (volcaniclastic, $n = 8$; diorite, $n = 22$) in the Luquillo Experimental Forest, Puerto Rico

Measurement	Soil type		Significance[a]
	Volcaniclastic	Diorite	*P*
Soil			
Organic matter (%)	9.41 ± 0.96	7.93 ± 0.36	0.086
Sand (%)	25.47 ± 3.23	63.47 ± 2.01	<0.001
Clay (%)	42.66 ± 5.13	9.43 ± 1.17	<0.001
Total nitrogen (mg g^{-1})	0.46 ± 0.08	0.14 ± 0.03	<0.001
Water-holding capacity (%)	66.50 ± 4.33	58.22 ± 1.32	0.020
Sediment runoff (g day^{-1})[b]	25.45 ± 8.50	80.86 ± 14.35	0.009
Litterfall (g m^{-2} day^{-1})	1.15 ± 0.30	0.61 ± 0.11	0.052

[a] Results of the MANOVA for soil variables is: Wilks' Lambda = 0.004, $P < 0.001$, $F_{5,24} = 1{,}177.33$), and univariate comparisons between soil type is based on $P < 0.05$

[b] Sediment runoff was collected in a 1-m long trap perpendicular to the landslide slope

cover ($P = 0.03$; $r^2 = 0.18$) and aboveground biomass ($P < 0.001$; $r^2 = 0.41$; Fig. 2), indicating that the variables in PC 1 influence two aspects of early plant succession on these landslides in the LEF. High values of PC 1 refer to high levels of soil clay, total N, and water-holding capacity, and low elevations. Therefore, low elevation landslides with high levels of clay, total N, and water-holding capacity, and low amounts of sand (also corresponding to volcaniclastic soil type; Table 2), accumulate greater aboveground biomass and plant cover than landslides without this combination of characteristics. Although PC 2 included an important indicator for seed dispersal and litterfall inputs

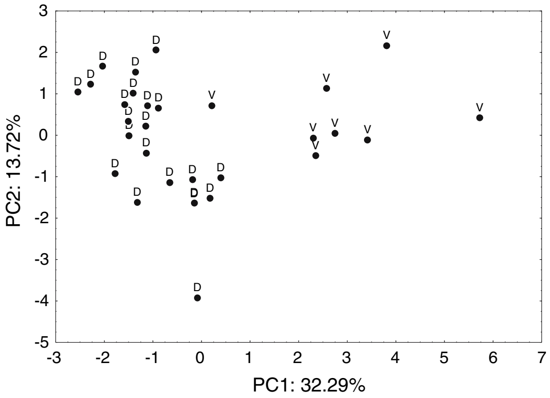

Fig. 1 Plot of individual landslides in the Luquillo Experimental Forest, Puerto Rico as discriminated by PC 1 and PC 2. Volcaniclastic (V) and diorite (D) landslides are well discriminated along PC 1. Axis percentages represent the amount of variation explained by each respective PC

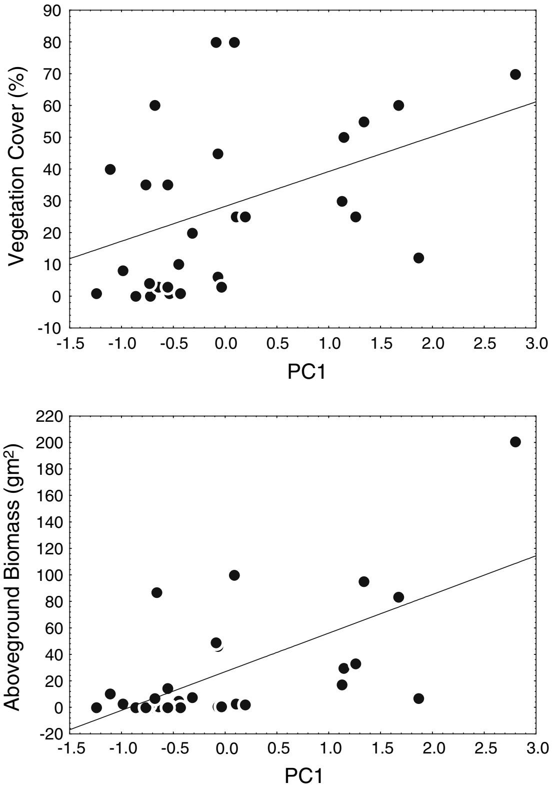

Fig. 2 Results of significant regressions of PCs on the variables that reflect initial plant colonization on 30 landslides in the Luquillo Experimental Forest, Puerto Rico. Positive values of PC 1 (*x*-axis) reflect high soil N, clay, and water-holding capacity, and low elevation and sand

to landslides (i.e., distance to forest edge), and PC 3 included an important indicator for slope stability, these PCs were not significantly correlated with any of the plant colonization response variables ($P > 0.05$).

When the two soil types were examined separately, it became apparent that the results of the first PCA were dominated by differences among these two soil types. On volcaniclastic soils, four PCs accounted for 86.76% of the variation in the data set (Table 3). Principal component 1 was dominated by variables related to soil characteristics of the landslides (excluding SOM and nitrogen), landslide size (distance to forest edge), and slope stability (average sediment runoff, slope; Table 3). Principal Component 2 was dominated by average soil movement, average litterfall, and total nitrogen (Table 3). Principal component 3 was dominated by slope and elevation, whereas PC 4 was dominated by canopy cover (Table 3). Multiple regressions revealed that the first four PCs accounted for a significant amount of variation in vegetation cover ($r^2 = 0.972$) with PC 1 ($P = 0.037$; $r^2 = 0.11$), PC 2 ($P = 0.004$, $r^2 = 0.23$), and PC 4 ($P = 0.015$, $r^2 = 0.60$) all being significantly correlated (Fig. 3). Multiple regression also revealed that the first four PCs accounted for a significant amount of variation in aboveground biomass ($r^2 = 0.896$), with PC 1 ($P = 0.037$, $r^2 = 0.44$) significantly correlated (Fig. 3). Principal Component 3 did not have significant associations with any variables related to initial plant colonization of volcaniclastic landslides. High values of PC 1 corresponded to high levels of sediment runoff, water-holding capacity, and clay, and large landslides with shallow slopes and low amounts of sand. High values of PC 2 corresponded to high levels of soil movement and low nitrogen. High values of PC 4 indicate more complete canopy cover. It should be noted that the first four PCs represent a greater percentage of the available PCs (relative to the full data set) given the reduced sample size of only $n = 8$ landslides that were volcaniclastic. This inflates the variation explained by the PCA although it does not necessarily have an effect on the r^2 values of regressions of individual PCs on the plant succession variables (see results for diorite soils where a reduced data set had no effect on inflating r^2 values).

On diorite soils, the first four PCs accounted for 65.98% of the variation in the data set (Table 4).

Table 3 Eigenvalues and factor-loadings for the first four principal components for eight volcaniclastic landslides in the Luquillo Experimental Forest, Puerto Rico

Variable[a]	PC 1	PC 2	PC 3	PC 4
Eigenvalue	4.56	2.82	2.37	1.53
% of total variance explained	35.05	21.69	18.26	11.76
Slope	**−0.670**	−0.110	**−0.659**	−0.277
Elevation	−0.260	0.426	**0.779**	−0.354
Distance to forest edge	**0.844**	−0.105	0.284	0.054
Average % canopy cover	−0.511	−0.132	0.459	**0.691**
Average litterfall	0.339	**−0.789**	0.199	−0.041
Microtopography index	0.197	0.514	−0.464	0.464
Average soil movement	−0.172	**0.909**	0.307	0.035
Average sediment runoff	**0.724**	0.096	0.236	0.516
Soil organic matter	0.442	0.232	0.492	−0.550
% sand	**−0.762**	−0.508	0.319	0.019
% clay	**0.830**	0.056	−0.502	−0.235
Total nitrogen	0.525	**−0.721**	0.284	0.054
Soil water-holding capacity[b]	**0.787**	0.195	−0.002	0.053

[a] The factor-loading cutoff (0.63) was based on the findings of Comrey (1973), and each variable equal to or exceeding that cutoff is shown here in bold

[b] Soil collections were from 0 to 10 cm depth

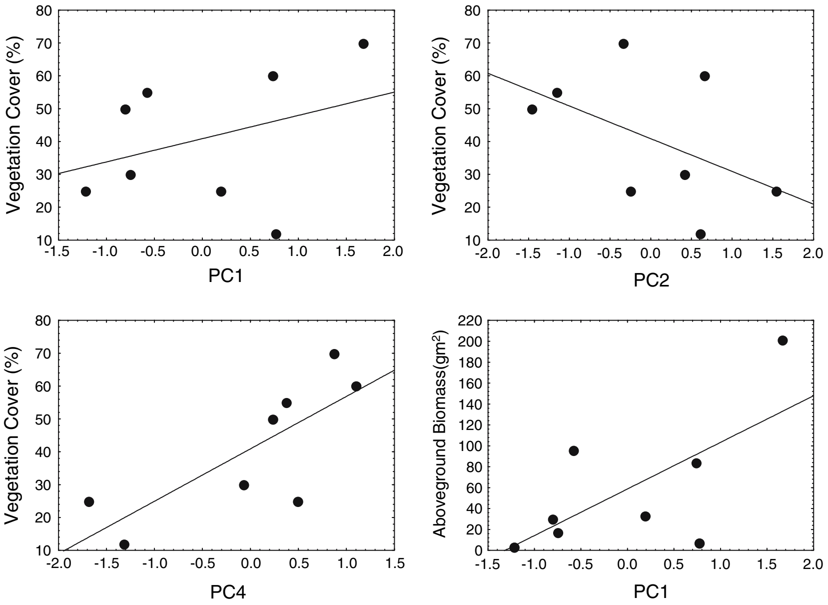

Fig. 3 Results of significant regressions of PCs on the variables that reflect initial plant colonization on eight volcaniclastic landslides in the Luquillo Experimental Forest, Puerto Rico. Positive values of PC1 (*x*-axis) reflect high levels of sediment runoff, water-holding capacity, and clay content, as well as landslides with shallow slopes, greater distance from the forest edge, and low sand content. High values of PC2 correspond with high levels of soil movement and low nitrogen. High values of PC4 indicate more complete canopy cover

Table 4 Eigenvalues and factor-loadings for the first four principal components for 22 diorite landslides in the Luquillo Experimental Forest, Puerto Rico

Variable[a]	PC 1	PC 2	PC 3	PC 4
Eigenvalue	3.04	2.57	1.61	1.36
% of total variance explained	23.35	19.78	12.41	10.44
Slope	0.604	0.110	−0.241	−0.440
Elevation	0.612	−0.140	−0.352	−0.192
Distance to forest edge	0.509	−0.343	−0.116	0.295
Average % canopy cover	−0.406	**0.682**	−0.225	−0.159
Average litterfall	−**0.726**	0.466	−0.098	−0.307
Microtopography index	−0.413	0.340	−0.004	0.047
Average soil movement	0.145	0.235	−0.462	**0.672**
Average sediment runoff	−**0.722**	−0.444	0.057	0.064
Soil organic matter	0.432	0.517	−0.156	−0.465
% sand	0.197	0.414	**0.753**	0.216
% clay	−0.253	−**0.795**	−0.360	−0.210
Total nitrogen	−0.353	−0.511	0.249	−0.334
Soil water-holding capacity[b]	−0.466	0.198	−0.599	0.210

[a] The factor-loading cutoff (0.63) was based on the findings of Comrey (1973), and each variable equal to or exceeding that cutoff is shown here in bold

[b] Soil collections were from 0 to 10 cm depth

Principal component 1 was dominated by litterfall and sediment runoff, PC 2 was dominated by canopy cover and percent clay, PC 3 was dominated by percent sand, and PC 4 was dominated by average soil movement (Table 4). Multiple regressions were only significant for belowground biomass and total biomass but only accounted for 34.4 and 31.0% of the variation, respectively, of these two variables. In both of these cases, only PC 4 was significant and these regressions were heavily influenced by high belowground biomass on one landslide. When this single point (landslide) was removed, the relationship was no longer significant. Therefore, on diorite landslides, there were no relationships between any of the soil or landslide characteristics and patterns of succession.

Despite the high sediment runoff from diorite landslides (Table 2), this and other slope stability measures had little impact on initial plant colonization on these landslides. In addition to the soil dichotomy clearly reflecting most measured soil parameters (Table 2), plant species composition also varied between soil type as vines, trees, and shrubs tended to dominate the volcaniclastic landslides (high soil clay, nitrogen, water-holding capacity, and low elevation), whereas herbs dominated the diorite substrate (Table 5).

Discussion

Landslides in the Luquillo Experimental Forest (LEF) with volcaniclastic soils containing high proportions of clay, low proportions of sand, high total N, and high water-holding capacity were colonized within 13 months by greater amounts of vegetation than diorite landslides without these characteristics. Soil type and elevation are directly correlated in the LEF (see Table 1), as all lower elevation forests and landslides (below 400 m a.s.l but often up to 600 m a.s.l) are dominated by relatively clay-rich volcaniclastic soils (Seiders 1971). The sandier diorite soils are only found in a large distinct patch at the upper portion of the mountain in the LEF (Seiders 1971). As the two different soil types are distributed at two different elevations, the high factor-loading for elevation is the result of elevation acting as a surrogate for soil type.

When the two main substrate types of the LEF are separated, slope stability indices and the distance to

Table 5 Vegetation characteristics (mean ± SE) on 13-month-old landslides with two different soil types (volcaniclastic, $n = 8$; diorite, $n = 22$) in the Luquillo Experimental Forest, Puerto Rico

Vegetation measurement	Soil type		Significance[a]
	Volcaniclastic	Diorite	*P*
Biomass (g m^{-2})			
Trees and shrubs	18.07 ± 9.65	1.40 ± 0.99	<0.001
Herbs	2.37 ± 1.88	7.72 ± 4.03	0.698
Vines	22.66 ± 10.19	1.57 ± 0.78	0.002
Graminoids	10.94 ± 5.53	2.94 ± 1.61	0.036
Ferns[b]	4.55 ± 1.79	0.92 ± 0.38	0.002
Bryophytes	0.12 ± 0.12	0.65 ± 0.43	0.436
Total aboveground	58.71 ± 23.57	15.28 ± 6.13	0.007
Total belowground	17.70 ± 6.48	41.75 ± 22.77	0.997
Total	76.41 ± 28.70	57.03 ± 23.93	0.227
Cover (%)			
Trees and shrubs	19.57 ± 6.24	2.20 ± 1.22	<0.001
Herbs	3.50 ± 1.80	13.29 ± 4.70	0.617
Vines	10.75 ± 4.12	1.50 ± 0.93	0.002
Graminoids	8.13 ± 3.31	3.65 ± 0.95	0.082
Ferns	9.71 ± 2.83	3.81 ± 2.07	0.011
Bryophytes	8.86 ± 3.69	9.25 ± 2.62	0.992
Total	40.88 ± 7.26	23.64 ± 5.71	0.031

[a] Results of the MANOVA for all variables listed in the biomass category (Wilks' Lambda = 0.463, $P = 0.038$, $F_{9,20} = 2.573$), and the cover category (Wilks' Lambda = 0.433, $P = 0.005$, $F_{7,22} = 4.113$)

[b] The fern category includes fern allies

the forest edge, combined with soil factors (particle size and water-holding capacity) predicted initial plant colonization on volcaniclastic landslides, whereas no measured variables predicted initial plant colonization on diorite landslides. These results contrast with previous hypotheses that organic matter (Guariguata 1990; Zarin and Johnson 1995a, b; Walker et al. 1996) is an important determinant of plant recovery on landslides. The lack of predictive variables on diorite landslides suggests that either we did not measure those variables that influence initial plant colonization or the diorite landslides were so similar in each of the measured variables that no single factor produced a detectable effect on plant establishment.

We expected organic matter deposited into landslides via litterfall to increase SOM and nutrients, as suggested for tropical wet forests (Vitousek and Sanford 1986). However, this was not the case in our study, or in the study by Shiels et al. (2006) that showed organic matter will only increase soil N and plant growth on recent landslides if it is in the form of forest soil, and not leaf litter. Little SOM remains after a landslide occurs (Zarin and Johnson 1995a, b; Walker et al. 1996), and litterfall is converted to SOM slowly due to slow decomposition rates on LEF landslides (Shiels 2006). Organic matter and associated nutrients such as N are critical for plant growth and survival on landslides (Dalling and Tanner 1995; Fetcher et al. 1996). Yet our study shows that smaller particle soils (i.e., clay) that can retain higher amounts of N (and water) more strongly contribute to initial (13 month) plant colonization on recent landslides than other measured variables such as SOM. Clay contains high concentrations of nutrients that are available for plant uptake (Zobel and Antos 1991; Sparks 2003) and retains more water than sandier soils (Sparks 2003), a likely benefit for successful plant establishment in severe landslide environments. Thus, for predicting initial vegetation colonization on landslides across the LEF, determining site concentrations of soil clay, N, and water-holding capacity is more useful than SOM levels.

Soil particle size on LEF landslides was the best predictor of the quantity of plants and composition of establishing plant life forms. Particle size is also important in other sites of primary succession, such as on landslides in Tanzania (Lundgren 1978) and on a glacial moraine in the North Cascade Mountains of Washington (Jumpponen et al. 1999), where coarse-textured soils appear to limit succession. Grubb (1986) suggested the importance of substrate particle size in determining which pioneer species establish on a given site. However, the association between particle size and early plant colonists may be less predictable in primary succession (Jumpponen et al. 1999; Walker and del Moral 2003; Walker et al. 2006). On LEF landslides, herbaceous vegetation dominates the coarser-grained (sandier) soils, whereas vines, pioneer trees and shrubs, ferns, and graminoids tend to colonize high-clay soils. Additionally, because the coarser-grained, diorite soil type is only found at the upper elevation of the LEF, elevation may also influence plant life-forms and biomass. For example, in Jamaica, vines dominate low elevation forests, but are absent in upper montane forests (Grubb and Tanner 1977). In the LEF, vines are present along the entire elevation gradient, but in different species composition and abundances (A. Shiels, personal observation). Altitudinal gradients, such as in the LEF, often experience marked changes in rates of ecosystem processes, such as decreased rates of plant production (e.g., litterfall) with increasing elevation (Waide et al. 1998), which is reflected in our study where lower elevation landslides (volcaniclastic) tended to have higher litterfall rates than upper elevation (diorite) landslides (Table 2). Therefore, separating the influence of soil type from elevation can be challenging, and our data supports the combination of these two important factors for predicting plant colonization.

We predicted that slope stability would influence the quantity and rate of establishing plants on LEF landslides, as a higher angle of repose should result in increased sediment runoff and associated plant propagule loss from the initially bare soils. Although the diorite soils had much greater sediment runoff than volcaniclastic soils, and soil movement and sediment runoff accounted for some of the variation in our dataset, slope stability did not influence initial plant establishment on diorite landslides. A similar result was found in an Alaskan landslide study (Lewis 1998). On volcaniclastic landslides, we found that elevated sediment runoff was associated with greater plant colonization (aboveground biomass and plant cover) and shallow slope, but soil movement was negatively associated with higher plant cover. Perhaps compact soils reduced both colonization and sediment loss while soil movement disrupted root growth. Adams and Sidle (1987) found heterogeneous surface mixing and soil compaction at multiple vertical positions on Alaskan landslides, and this may affect sediment runoff irrespective of landslide slope. Additionally, higher aboveground biomass on shallower, more erosive, volcaniclastic landslide slopes may be a result of a greater abundance of vines compared to other plant life forms.

The proximity to the forest-landslide edge influenced initial plant cover and aboveground biomass on volcaniclastic landslides. Since the forest is an important source of both organic matter and plant propagules (e.g., seeds), and seed rain in the LEF was previously shown to decrease from forest to landslide (Walker and Neris 1993), it was surprising that elevated plant colonization on volcaniclastic landslides was associated with greater distances from the forest edge. Perhaps the large quantities of highly mobile seed rain (mainly graminoids) that reach most LEF landslides (Shiels and Walker 2003), or competition from nearby forest plants on these relatively small landslides (compared to others studied in the LEF: Myster et al. 1997; Li et al. 2005) may have influenced the relative importance of proximity to edge when predicting initial plant colonization.

Initial vegetation colonization can now be more easily predicted on landslides in the LEF in general, and within a given soil type. In contrast to previous hypotheses, SOM is a less useful predictor for initial plant colonization and succession on LEF landslides. Geologic history largely contributes to vegetation recovery on landslides, as the volcaniclastic parent material provides a different substrate for soil formation than the diorite parent material. Volcaniclastic parent material is chronologically older than the diorite, and therefore has experienced a longer weathering period resulting in higher concentrations of soil clay, which retains more resources that are critical for plant growth (i.e., N and water) when compared to the sandier, diorite soils. The result of these geologic conditions shows that within perhaps the most severe disturbance in the LEF, initial vegetation recovery will be greater, and the plant life forms will be different, on the volcaniclastic landslides because of soil type specific properties (high clay content, N, and water-holding capacity). Uncertainties about forecasting initial succession on diorite landslides still remain. Diorite landslides are very prone to post-landslide erosion, and because of the less rampant plant colonization of these sandier, upper elevation landslides, land managers seeking to accelerate vegetation recovery and arrest post-landslide erosion on LEF landslides should focus their efforts on increasing favorable microsites on diorite landslides. Our ability to predict plant succession on landslides is constrained to the first year following disturbance, yet this initial stage is often the most important in shaping subsequent stages (Walker and Chapin 1987; Tagawa 1992; Eriksson and Eriksson 1998; Walker and del Moral 2003). Therefore, our findings provide a better understanding of early succession on landslides and the importance of underlying geology and soil type in influencing plant establishment.

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Appendix

Appendix 1 Site characteristics for 30 landslides in the Luquillo Experimental Forest, northeastern Puerto Rico (V = volcaniclastic, D = diorite)

Landslide	Soil type	Slope (degrees)	Elevation (m)	Distance to forest edge (m)	Area (m^2)	Average canopy cover (%)	Average litterfall (g m^{-2} day^{-1})	Microtopography index	Average soil movement (cm day^{-1})	Average sediment (g day^{-1})	Soil water-holding capacity (g H_2O g $soil^{-1}$)	Soil organic matter (%)	Sand (%)	Clay (%)	Total soil N (mg N g $soil^{-1}$)
1	V	21	224	3.0	240	58	0.79	127.3	0.01	72.5	64.6	9.85	18.8	52.5	0.37
2	V	32	219	3.5	81	41	0.65	116.2	0.00	11.7	75.3	9.77	11.3	65.0	0.33
3	V	42	166	1.2	324	58	0.50	123.0	0.01	9.1	64.9	8.01	26.3	43.8	0.31
4	V	38	152	2.5	336	69	2.67	114.5	0.00	12.8	47.8	7.70	35.0	32.5	0.41
5	V	5	220	5.0	1125	64	1.96	117.3	0.02	54.3	90.2	10.37	16.3	53.8	0.79
6	V	28	215	2.0	150	66	0.80	112.2	0.00	12.1	66.3	5.64	36.3	33.8	0.72
7	V	21	815	2.6	54	52	1.59	112.9	0.09	17.6	62.7	14.97	31.3	41.3	0.61
8	V	23	825	2.0	68	75	0.20	116.8	0.00	13.5	60.1	8.99	28.8	18.8	0.15
9	D	50	780	3.5	238	43	0.08	112.9	0.02	21.8	56.9	9.98	67.5	6.3	0.04
10	D	40	740	3.4	480	22	0.04	113.1	0.00	81.7	56.3	8.20	53.8	23.8	0.37
11	D	36	698	3.6	152	73	0.91	131.7	0.01	33.3	69.9	7.48	71.3	8.8	0.28
12	D	25	672	2.0	27	57	1.26	118.6	0.02	115.1	62.1	3.52	53.8	15.0	0.11
13	D	37	661	5.0	238	50	0.86	118.5	0.02	76.4	55.8	7.68	67.5	5.0	0.00
14	D	27	644	5.0	245	29	0.22	112.7	0.01	60.9	47.3	7.57	68.8	7.5	0.25
15	D	40	647	1.6	49	85	0.74	117.9	0.01	41.6	59.5	8.31	73.8	5.0	0.00
16	D	30	677	1.6	189	8	0.64	127.6	0.02	92.2	54.7	8.60	70.0	5.0	0.02
17	D	31	679	3.4	180	14	0.09	117.9	0.01	231.9	63.2	3.55	58.8	18.8	0.22
18	D	44	680	1.8	274	14	0.03	113.8	0.00	52.1	41.5	7.05	75.0	10.0	0.31
19	D	38	669	2.0	432	43	0.94	114.9	0.02	96.0	56.3	8.94	66.3	6.3	0.09
20	D	46	654	2.4	87	45	0.50	115.4	0.00	55.9	57.9	8.33	66.3	11.3	0.04
21	D	48	663	1.8	316	71	2.00	115.0	0.00	43.4	61.0	10.68	58.8	11.3	0.38
22	D	11	670	1.0	70	55	0.55	112.8	0.01	137.7	70.2	7.33	73.8	2.5	0.32
23	D	44	656	2.5	70	54	0.25	116.3	0.00	29.9	61.0	9.14	58.8	5.0	0.01
24	D	25	668	1.0	32	86	1.43	135.3	0.02	73.4	54.0	8.01	66.3	8.8	0.15
25	D	43	668	1.2	48	41	1.14	117.0	0.03	248.2	61.4	9.45	46.3	10.0	0.07
26	D	36	660	1.6	269	67	0.83	112.7	0.01	189.2	61.2	6.64	58.8	16.3	0.31
27	D	30	782	2.9	190	33	0.16	120.3	0.03	61.1	60.0	8.88	43.8	13.8	0.03
28	D	38	777	1.7	128	51	0.32	117.6	0.01	6.8	58.1	8.01	53.8	8.8	0.03
29	D	44	752	3.1	126	42	0.36	113.7	0.01	25.5	56.7	8.43	63.8	8.8	0.11
30	D	42	757	2.4	111	45	0.06	114.1	0.00	5.1	55.8	8.84	80.0	0.0	0.04

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