Plant Soil (2008) 313:205–216
DOI 10.1007/s11104-008-9692-3

REGULAR ARTICLE

Post-disturbance erosion impacts carbon fluxes and plant succession on recent tropical landslides

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Received: 10 December 2007 / Accepted: 10 June 2008 / Published online: 1 July 2008

Abstract Tropical landslides are suitable locations to study short-term carbon (C) fluxes because of the rapid changes that occur for the first few years following initial disruption of the slope. Because of the high heterogeneity among landslide soils and plant re-colonization patterns, we measured C fluxes from 30 landslides in the Luquillo Experimental Forest in northeastern Puerto Rico from 8–13 months after landslide formation. Post-landslide erosion resulted in significantly higher soil output on dioritic than on volcaniclastic soils, with no temporal decline in soil output during the study. Much more C was found in landslide soils than in plant biomass, and we estimate that 6–24% of the soil C standing stock would erode from our plots within 1 year. Even the relatively small amount of C in plant matter was in flux, with four to five times plant C standing stock deposited into the plots as plant litter and two times standing stock leaving our plots in 1 year. This rapid turnover of C is indicative of highly unstable substrates that likely stabilize over successional time. We combined our short-term study with past chronosequence studies to project long-term carbon movement in landslides. We suggest that landslides in Puerto Rico represent a net down slope movement of C despite deposition from surrounding forest soils, litter from the surrounding landscape and in situ successional re-growth.

Keywords Carbon pools · Disturbance · Litterfall · Nitrogen · Revegetation · Succession

Responsible Editor: Klaus Butterbach-Bahl.

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Introduction

Much is known about the physical aspects of landslides (Bonnard et al. 2004; Sidle and Ochiai 2006; Sassa et al. 2007) and there is limited but growing information about landslide ecology, particularly how plant succession occurs on landslides (Walker et al. 1996; Restrepo and Vitousek 2001; Shiels et al. 2006; Cammeraat et al. 2007). However, information is still scarce on how the geology and ecology of landslides are linked, specifically through soil erosion and carbon (C) transfers. Determining rates of soil erosion can elucidate soil development and nutrient budgets on individual landslides (Zarin and Johnson 1995a, 1995b; Shiels et al. 2006), along ridge-to-valley toposequences (Silver et al. 1994) and at forest-wide scales (Wilcke et al. 2003). Post-disturbance soil erosion can impede physical amelioration of landslides (Chacón et al. 1996; Senneset 1996) and revegetation through succession (Walker et al. 1996; Walker et al. 2007; Shiels et al. 2008).

New landslides in the Luquillo Experimental Forest (LEF) in Puerto Rico impact 1–3% of the surface of the forest every 100 years (Walker et al. 1996). These landslides are subjected to high rates of soil erosion, even months after the initial disturbance, yet these rates have rarely been quantified. In the LEF, as elsewhere (Dai and Lee 2002; Espizua and Bengochea 2002), substrate characteristics commonly influence the frequency, density and stability of landslides. Landslides in the LEF are less common on generally low-elevation, clay-rich, more stable soils (Ultisols derived from weathered volcaniclastic parent material) than on generally higher elevation, sandy, erosive soils (Inceptisols derived from weathered quartz–diorite parent material; Seiders 1971; Larsen and Torres-Sánchez 1995; Shiels et al. 2008). These soils are henceforth called volcaniclastic and dioritic soils, respectively, to reflect their different origins. Potential differences in soil erosion and C fluxes between these two types of soils have rarely been examined (Larsen et al. 1999) and their implications for subsequent successional dynamics are unknown.

The link between landslide erosion and plant succession is complex (Walker and del Moral 2003) but plants generally reduce surface and near-surface erosion, at least to their rooting depth (Cammeraat et al. 2007). How rapidly vegetation develops on landslides is likely a combination of substrate stability and fertility (Walker et al. 1996; Larsen et al. 1999), particularly soil N and clay content (Shiels et al. 2008). On Puerto Rican landslides, soil N, P, K and Mg can return to levels in adjacent moist tropical forests in <50 years (based on a chronosequence approach; Zarin and Johnson 1995b). However, C was slower to recover and may take 200–500 years (Zarin and Johnson 1995b; Walker et al. 1996). Slumping of forest soil can increase C in post-landslide soils more rapidly than plant litter, as experimentally demonstrated by Shiels et al. (2006). Plant growth ultimately increases soil C, yet on landslides plant growth can be highly spatially variable both within and between landslides (Adams and Sidle 1987; Shiels et al. 2006; Geertsema and Pojar 2007). This variability reflects not only heterogeneous conditions of soil stability and fertility but also the spatially variable conditions for dispersal (Walker and Neris 1993; Shiels and Walker 2003) and colonization (Walker 1994; Walker et al. 1996).

Regular monitoring of a large number of landslides can help clarify the relative importance of erosion and C inputs and outputs for plant succession. In this paper, we describe the spatial and temporal dynamics of C and other soil variables on 30 recent landslides from 1 m^2 plots during a 6-month period. We extend the study by Shiels et al. (2008) that used soil factors to predict plant colonization by focusing in this study on measuring and predicting C fluxes over time and contrasting the landslide C pools on the two distinct soil types in the LEF. Specifically, we ask: (1) Do C outputs in soil decrease with time and are they greater for landslides on dioritic than volcaniclastic soils? (2) Are C inputs from plant litter greater than C outputs from litter and how do litter C fluxes vary with time and soil type? (3) Is the quantity of soil output (i.e., erosion) predictable based on measured soil variables? (4) How do C fluxes compare with total C stocks in both plants and soils? Finally, we use data from this study and longer-term studies to model how landslides represent a net down slope movement of C despite regular inputs of C and successional re-growth.

Methods

We conducted our study in the Luquillo Experimental Forest (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 are 21–25°C (Brown et al. 1983). The LEF ranges in elevation from 150 m to just over 1000 m, and includes four major vegetation zones occurring along an altitudinal gradient. The tabonuco (*Dacryodes excelsa*) 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 approximately 750 m a dwarf forest occurs and *Tabebuia rigida* and *Ocotea spathulata* are the dominant trees. Palm forests (*Prestoea acuminata*—formerly *P. montana*) are interspersed throughout the other three forest types. Vegetation nomenclature follows Liogier and Martorell (1982) and Taylor (1994).

We examined soils on 30 landslides randomly chosen from 69 that were caused by a storm in the LEF in April 2003 and that were within 200 m of a road. The landslides ranged in slope from 5–50° (mean±SE=33.8±2.0), in size from 27–1,125 m^2 (mean±SE=211±38) and in elevation from 152 m to 825 m a.s.l. (mean±SE=603±39). Landslides were found on both volcaniclastic (n=8) and dioritic (n= 22) soils in all four forest types. In October 2003, we randomly located one 1×1 m plot within the landslide chute (the central area of highest erosion within a landslide; Guariguata 1990) of each of the 30 landslides. Plot edges were perpendicular and parallel to the direction of the slope, and they were at least 1 m (mean±SE=2.54±0.21) from any forest-landslide edge. Larger plots were not feasible due to logistical concerns of soil processing; our large sample size provided an adequate test of our key comparison of soil types.

Soil output (surface erosion, slopewash) from each plot was measured biweekly from December 2003 to May 2004 (6-month period, 8–13 months following landslide formation) at the base of each plot using one 100×8×7 cm deep, open-top plastic rain gutter placed perpendicular to the slope and tilted to allow flow into a plastic collection bucket (a modified Gerlach trough; Gerlach 1967 as cited in Larsen et al. 1999). Our plots were otherwise unbounded to avoid edge effects. We calculated soil erosion with and without accounting for the total likely catchment area above our 1 m wide trough, but present our analyses based on the latter (an assumption of a 1 m^2 catchment area) because of the numerous errors possible when calculating catchment area (Larsen et al. 1999). We compared biweekly sums of soil output to sums of biweekly precipitation data from the Bisley Watershed (http://luq.lternet.edu/data/lterdb29/metadata/lterdb29.htm), the monitoring station closest to the majority of our plots. From each biweekly collection we analyzed soil dry mass after removing coarse particles >0.2 cm in diameter; we also measured the mass of all easily separable litter (organic matter >0.5 cm in diameter). We analyzed soil organic matter (SOM; % loss on ignition) and total Kjeldahl N (sulphuric acid digestion followed by colorimetric analysis; Alpkem 1992), both pooled monthly to reduce costs (n=6 for each of the 30 landslides). We did not measure dissolved organic C or N in water flowing off the plot, or C losses through microbial respiration, although the latter values are likely small on <1 year old landslides (H. Ruan, personal observation; A. Shiels, unpublished data).

In addition to dry mass of litter outputs removed from the soil, we determined dry mass of all net litter inputs (not size-limited) onto the soil surface of each 1 m^2 plot biweekly from December 2003 to May 2004. We pooled litter inputs originating from plants growing inside each plot (only between 4% and 15% of the total litter inputs from dioritic and volcaniclastic soils, respectively) with the bulk of litter inputs that originated from outside but were collected from each plot. An adjacent 1×1 m "control" plot did not indicate any impact of litterfall collection on SOM or vegetation parameters (Shiels et al. 2008).

Soils were sampled from three pooled soil cores (1.9 cm diameter and 10 cm deep; 28.3 cm^3) taken in May 2004 from random locations within each plot and analyzed (after removal of any rocks, roots or litter that exceeded 0.2 cm diameter; the organic portion of this fraction never exceeded 1% of total mass) for SOM (% loss on ignition), total Kjeldahl N (Alpkem 1992), pH, bulk density (gram per cubic centimetre dry soil) and percent sand, silt and clay (hydrometer method; Sheldrick and Wang 1993). We took an additional soil core (7 cm diameter to 10 cm depth; 384.8 cm^3) to determine soil water holding capacity (wet − dry)/dry mass×100, where wet mass was taken after 10 min of draining saturated soils). Also in May 2004, we measured the dry mass of all live aboveground plant material (henceforth shoots) and all roots (live plus dead, >1 mm diameter) to 16 cm depth from each plot.

Finally, we develop a conceptual model of pre- and post-landslide C dynamics on a hypothetical landslide, based on data from this study as well as from several short- and long-term studies and previous models of landslides in the LEF in order to suggest how landslides contribute to landscape-level C dynamics.

Data analysis

All SOM measurements were divided by 1.724 to convert to organic C (Chancy and Swift 1984). Plant dry mass was divided by 2.0 to convert to organic C (Gifford 2000) when comparing total C fluxes. Carbon and N in soil output and soils were expressed on an areal basis by multiplying concentrations by soil bulk density. Soil and plant litter fluxes across 12 sample dates (11 for litter outputs) were compared between volcaniclastic (n=8) and dioritic (n=22) landslides and temporal differences in soil output and litter inputs and outputs were determined with repeated measures ANOVA. Because several of the measured soil and plant variables were closely related and often correlated, these variables (e.g., soil, soil C, soil N and litter) were entered into a single MANOVA before comparing each variable individually for differences between soil type using t tests. Similarly, a MANOVA, followed by individual t tests was performed for all related soil variables to test for differences between soil types.

Principle components analysis (PCA), followed by linear regressions, was conducted in order to determine which measured variables might predict soil output. This analysis utilized nine variables that we predicted to be important for soil output on the 30 landslides (bulk density, sand, silt, clay, water-holding capacity, slope, shoot and root biomass, and litterfall). Because of the high co-linearity among the nine variables, we used PCA to reduce the number of variables to a smaller number of variables (PCs) that were orthogonal. Following PCA, we used a factor loading cutoff of 0.63 and higher to assign significance of a particular variable with a PC (Comrey 1992; Shiels et al. 2008). We then used PCs to calculate factor scores for each landslide and used the factor scores in linear regression analysis to test whether PCs correlated with mean soil output. After conducting this analysis on the 30 landslides used in this study collectively, we also conducted two additional PCAs (one on each of the two soil types) in order to determine if soil output could be predicted by the nine variables once soil type had been accounted for. Linear regression on log-transformed data was also used to determine if precipitation influenced soil output. For each analysis, all variables were either log or square root transformed in order to meet assumptions of normality and equal variance. All analyses were conducted using SPSS (SPSS 1998). Significance was determined at P<0.05 and means are presented ±S.E.

Results

Soil and plant litter fluxes varied between volcaniclastic and dioritic soils (MANOVA: Wilks' lambda=0.21, $F_{4,25}$=27.93, P<0.001). Soil output was higher for dioritic than volcaniclastic soils during most of the 6-month study period (Fig. 1a; repeated measures ANOVA: time by soil type: $F_{11,308}$=3.49, P=0.015; time: $F_{11,308}$=27.06, P<0.001; soil type: $F_{1,28}$=7.66, P=0.010). When mean values were combined across time, outputs of soil and soil C from dioritic soils were 3.3 and 2.7 times higher, respectively, than from volcaniclastic soils, but N outputs in soils from the two types of landslides were similar (Table 1). Litter outputs and litter inputs were similar between soil types. Biweekly precipitation sums (mean±SE=168±34 mm; range=8–363 mm) never explained more than 25% of the variance in soil output (linear regression: volcaniclastic: df=11, P=0.38, r^2=0.08; dioritic: df=11, P=0.09, r^2=0.25).

Litter inputs generally increased with time ($F_{11,308}$=3.90, P=0.005; time by soil type interaction $F_{11,308}$=2.79, P=0.002; Fig. 1b), but there was no effect of soil type with the repeated measures ANOVA (volcaniclastic vs. diorite; $F_{1,28}$=2.881, P=0.101). There were also no significant temporal patterns or soil type differences for litter output (data not shown). Litter inputs were greater than litter outputs within both volcaniclastic ($F_{1,42}$=6.47, P=0.023) and dioritic ($F_{1,42}$=5.61, P=0.023) soils (Table 1).

Volcaniclastic soils differed in several ways from dioritic soils (MANOVA: Wilk's lambda=0.12, $F_{12,17}$=10.27, P<0.001; Table 2) and they had higher C (areal basis only), N (areal and concentration basis) and clay content. Volcaniclastic soils also held more water and supported more shoot biomass than dioritic soils (Table 2). Dioritic soils were very sandy (63%) and had less than one third the N found in volcaniclastic soils, as shown by their different C:N ratios (volcaniclastic, 124; dioritic, 318).

Following PCA, three PCs had eigenvalues >1.0, which collectively explained 69.7% of the variation for the nine variables across 30 landslides. For PC1 (which explained 36.2% of the variation), four variables had PC scores >0.63 (sand, clay, water-holding capacity and shoot biomass). Despite the PCA explaining some of the variation in our data set, the PC scores did not predict soil output (linear regression; P>0.05). Similarly, the two additional

Fig. 1 Soil outputs from (**a**) and litter inputs into (**b**) 1 m^2 plots on volcaniclastic (n=8) and dioritic (n=22) soils on 8–13 month old landslides in Puerto Rico (g m^{-2} day^{-1}; mean±SE). Soil outputs were collected in 1 m wide gutters at the base of each plot

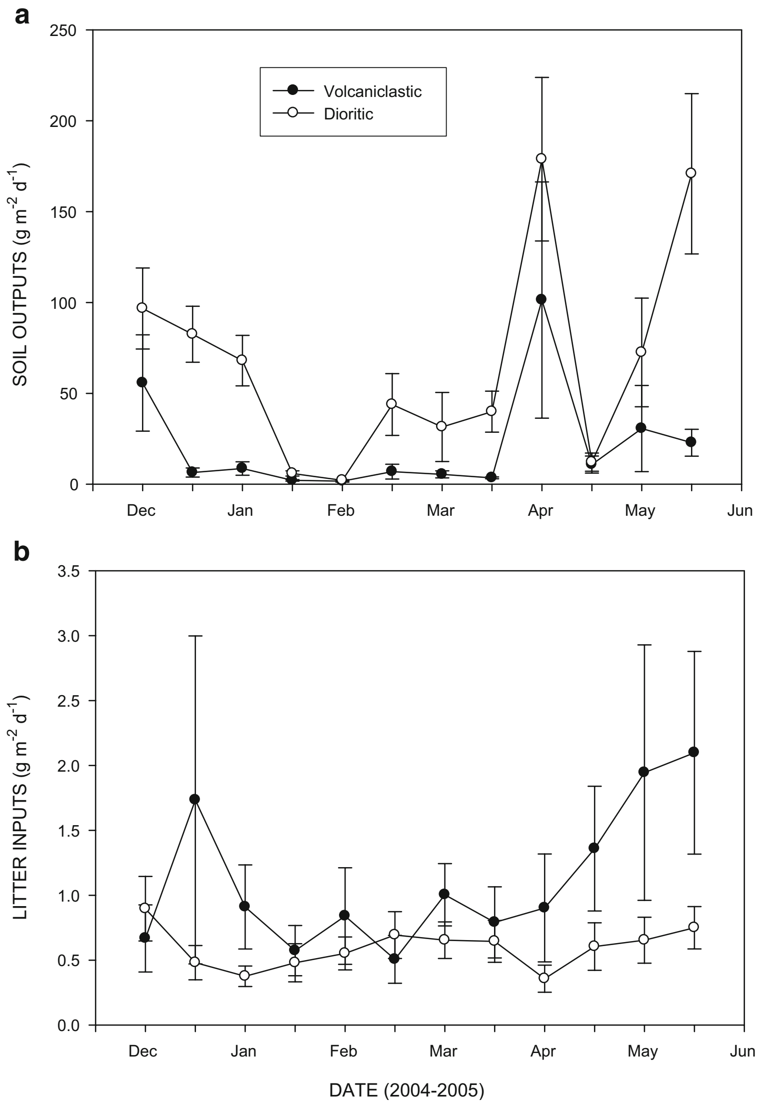

Table 1 Soil and plant litter fluxes on landslides in the LEF, northeastern Puerto Rico (mean±SE; n=8 volcaniclastic and 22 dioritic landslides using means of 12 biweekly samples for soil and litter inputs, means of 11 biweekly samples for outputs and means of 6 monthly composite samples for soil C and N)

Factor	Volcaniclastic	Dioritic	*F* value	*P* value
Outputs (g m^{-2} day^{-1})				
Soil	20.47±8.54	67.35±13.83	5.58	**0.025**
Soil C	1.12±0.47	3.10±0.64	4.39	**0.045**
Soil N	0.94±0.39	0.94±0.19	0.01	0.905
Litter	0.41±0.20	0.30±0.08	0.64	0.43
Inputs (g m^{-2} day^{-1})				
Litter	1.11±0.32	0.59±0.11	3.57	0.07

Litter inputs were collected from within each 1 m^2 plot. Soil and litter outputs were collected in 1 m long gutters at the base of each square metre plot. F and P values are shown for each t test comparing volcaniclastic and dioritic landslides (df=1, 28 for each) after MANOVA for all related factors. Significant P values are in bold.

Table 2 Soil characteristics (0–10 cm depth) and final plant harvest (roots to 16 cm depth) on eight volcaniclastic and 22 dioritic landslides in the LEF, northeastern Puerto Rico in May 2004 (mean±SE)

Factor	Volcaniclastic	Dioritic	*F* value	*P* value
Soils				
Carbon (mg g^{-1})	54.58±5.57	46.00±2.09	3.17	0.086
Carbon (g m^{-2})	6,217±698	4,680±231	7.47	**0.011**
Nitrogen (mg g^{-1})	0.46±0.08	0.14±0.03	17.91	**<0.001**
Nitrogen (g m^{-2})	50.33±7.21	14.73±3.01	29.28	**<0.001**
pH	4.48±0.29	4.39±0.12	0.10	0.753
Bulk density (g cm^{-3})	1.13±0.06	1.11±0.03	0.23	0.636
Particle size (%)				
Sand	25.47±3.23	63.47±2.01	91.81	**<0.001**
Silt	31.87±3.08	27.10±1.55	2.41	0.132
Clay	42.66±5.13	9.43±1.17	69.88	**<0.001**
Water-holding capacity (%)	66.50±4.33	58.22±1.32	6.05	**0.020**
Plants (g m^{-2})				
Shoots	58.71±23.64	15.28±6.13	8.48	**0.007**
Roots	17.70±6.48	41.75±22.77	<0.01	0.997
Total plants	76.41±28.70	57.03±23.93	1.53	0.227

F and *P* values are shown for each *t* test comparing volcaniclastic and dioritic landslides (*df*=1, 28 for each) after MANOVA for all related factors. Significant *P* values are in bold.

PCAs specific to each soil type found no variables that predicted soil output.

Carbon fluxes (but not standing stocks) varied between soil types. Total fluxes in g C m^{-2} day^{-1} for soil outputs and for litter inputs and outputs, respectively were 1.12, 0.55 and 0.20 (volcaniclastic) and 3.10, 0.29 and 0.15 (dioritic). Both volcaniclastic and dioritic soils (0–10 cm deep) lost more C per day (mostly in soil erosion) than was added by litter inputs, even though litter inputs on both soil types were twice the percentage of total C as litter outputs (Fig. 2). Total standing stocks of C (volcaniclastic, 6,255 g C m^{-2}; dioritic, 4,708 g C m^{-2}) were almost entirely in soils (6,217 and 4,680 g C m^{-2}) rather than in plant matter (38.2 and 28.5 g C m^{-2}; Table 2). The high fluxes would result in the loss of 6.5% (volcaniclastic) to 24.2% (dioritic) of the stock of soil C if our daily rates were extrapolated unchanged to a year. Carbon in litter outputs were nearly two times plant standing stocks for both soil types and C in litter inputs were five (volcaniclastic) and nearly four times (dioritic) plant standing stocks each year.

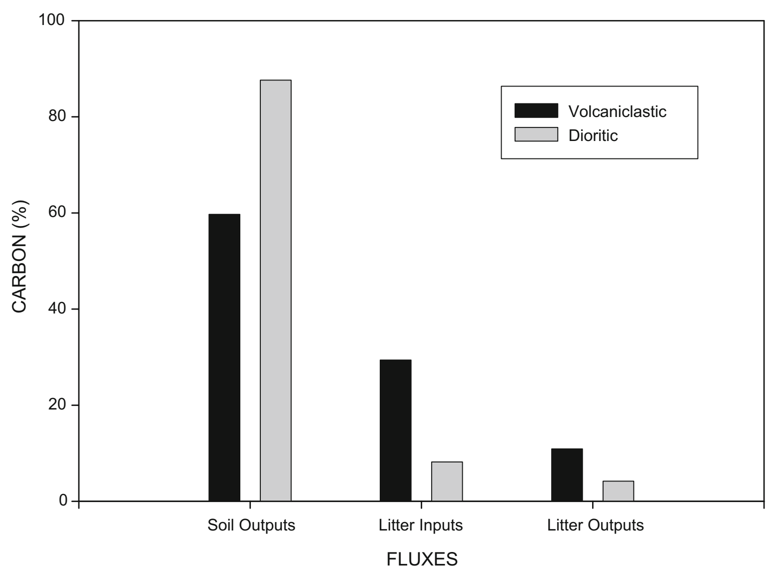

Fig. 2 Distribution of C within each soil type (volcaniclastic, dioritic; 0–10 cm depth) from three measured pools: outputs of soil and litter and inputs of litter. Proportions of total C within each soil type are based on means (g C m^{-2}) of biweekly measurements (December 2003–May 2004) from 1 m^2 plots on 8–13 month old landslides in Puerto Rico

Discussion

Our evaluation of C fluxes on 8–13 month old Puerto Rican landslides demonstrates that despite inputs from eroding soils at forest edges, litter from the surrounding forest and in situ plant growth, post-disturbance erosion results in a net down slope loss of C. Litter inputs were substantial (and two to three times higher than litter outputs) but 60–85% of C was lost through soil erosion. Such high erosion rates clearly impede stabilization and colonization by plants and prolong the disruptive effects of the initial landslide disturbance. Soil type, rates of soil output and plant colonization dynamics are primary influences on the persistence of landslide erosion in Puerto Rico and the recovery of C lost through landslides.

Larsen and Simon (1993) have established a close link between landslide formation in the LEF and the amount of rainfall over a given time period. Most landslides in the LEF can be traced to specific storm events such as Hurricane Hugo in September 1989 (Larsen and Torres-Sánchez 1992) or the April 2003 storm that triggered the landslides in this study (Shiels et al. 2008). However, we did not find a strong relationship between biweekly sums of precipitation at a nearby field station and biweekly measures of soil output in this study of post-disturbance erosion on existing landslides. Rainfall is highly spatially variable in the LEF (Brown et al. 1983) and other variables (e.g., soil saturation and vegetation cover) can be important in both triggering landslides and contributing to post-landslide erosion. The relatively short time span of our study did encompass four periods with high rainfall (early December, late February, late April and late May) when biweekly rainfall sums exceeded long term means (Brown et al. 1983). These periods accounted for 38% and 39% of soil outputs for volcaniclastic and dioritic soils, respectively, suggesting that substantial proportions of soil erosion from landslides are not linked to major precipitation inputs. Rainfall conditions required to trigger a landslide are more easily identified than those conditions that promote ongoing erosion.

Soil type had a clear impact on erosion rates on our landslides. Recently exposed dioritic soils on landslides in the LEF did erode more readily than volcaniclastic soils, as we expected (Larsen et al. 1999; Shiels et al. 2008).

Both soil types showed broadly similar temporal patterns of soil output but dioritic soils peaked at higher rates. Neither soil type showed any steady decline in soil output during our 6-month study of 30 landslides, unlike the decline Larsen et al. (1999) found in a 4-year study of two LEF landslides. Long-term soil stabilization is likely to be faster on the more fertile, less erosive volcaniclastic soils (Walker et al. 1996), but high variation among and within landslides suggests rates of stabilization and succession also will vary (Shiels et al. 2006).

Soil output rates vary with age of landslide, surrounding land use and methods for measuring soil movement. Our rates of output for volcaniclastic and dioritic soils (20 and 67 g m^{-2} day^{-1}=7.3 and 24.4 kg m^{-2} $year^{-1}$, respectively) on 8–13 month old landslides were much larger than data from Larsen et al. (1999) on two LEF landslides (0.03–0.12 kg m^{-2} $year^{-1}$ for a 4-year average; 0.10–0.35 kg m^{-2} $year^{-1}$ for the first year). Land use can impact soil output, yet both our study and that of Larsen et al. (1999) studied landslides with similar land use history within the LEF. Nevertheless, the young landslides in our study eroded more than Puerto Rican slopes under cultivation (1.3–1.6 kg m^{-2} $year^{-1}$; Smith and Abruña 1955) or associated with reservoir construction (0.3–0.9 kg m^{-2} $year^{-1}$; Gellis et al. 1999) or forest clearings in Jamaica (0.5–1.0 kg m^{-2} $year^{-1}$; McDonald et al. 2002).

Soil output values vary greatly among studies depending on catchment estimates. Larsen et al. (1999) estimated the likely catchment area above their Gerlach troughs while we did not because several fold errors are possible from local microtopographic variation, vegetative cover, rainstorm intensity and many other factors. Analysis of our data with estimated catchment areas above each plot reduced our soil output rates to 2 and 5 g m^{-2} day^{-1} (or 0.7 and 1.8 kg m^{-2} $year^{-1}$) for volcaniclastic and dioritic soils, respectively, placing our data well within the range of the other studies mentioned but still higher than Larsen et al. (1999). Absolute amounts of soil erosion are difficult to determine, as bounded plots have other problems (enhanced surface erosion or scour at plot boundaries; Larsen et al. 1999). However, our conclusions about relative amounts of C inputs and outputs between the two types of landslides remained unaltered whether plots or catchments were used.

Plant colonization can also impact the persistence of erosion both through indirect influences on litter inputs and outputs and soil C content and through direct influences on stabilization through root growth and reduction of rain impacts. Litter inputs and outputs did not differ between volcaniclastic and dioritic soils, although litter inputs increased on both types of landslides over the 6 month study period and it appears likely that litter inputs on volcaniclastic soils will exceed litter inputs on dioritic soils over time, as is typical of less disturbed forests growing on such substrates (Lodge et al. 1991). The facilitative effects of litter inputs on soil fertility and plant growth are often delayed at least 1 year on recent LEF landslides (Shiels et al. 2006), which is probably a result of slow decomposition rates (Shiels 2006). Our litter input values (1.11 and 0.60 g m^{-2} day^{-1}=405 and 219 g m^{-2} $year^{-1}$) for volcaniclastic and dioritic soils, respectively, were 3.4–6.2 times higher than data from 0.25 m^2 litter traps on the two 1–4 year old (but smaller) landslides studied by Larsen et al. (1999; 65 g litter m^{-2} $year^{-1}$). While landslide age, size (Walker and Neris 1993), spatial variance in litterfall (Burghouts et al. 1998) and adjacent forest species composition (Lodge et al. 1991) may explain the discrepancy in our two data sets, the most likely cause is the 50% reduction and gradual recovery of forest litterfall following Hurricane Hugo in 1989 (Scatena et al. 1996). Larsen et al. (1999) sampled 2–6 year after the hurricane while we sampled 14 year later. Our litterfall input data more closely resemble LEF forest litterfall from Larsen et al. (1999; 333–918 g m^{-2} $year^{-1}$), or immediately following Hurricane Hugo (230 g m^{-2} $year^{-1}$; Scatena et al. 1996).

Litter output reflects the relative stability of a landslide and may account for substantial C loss from landslides via litter suspended in eroding soils. Our litter output values on landslides (0.41–0.30 g m^{-2} day^{-1}=150–109 g m^{-2} $year^{-1}$) greatly exceeded both 1–4 year old landslides (2.5 g m^{-2} $year^{-1}$) and LEF forest plots (4.3–8.1 g m^{-2} $year^{-1}$; Larsen et al. 1999). Young landslides lack the usual litter retention mechanisms that are common in tropical forests, including fungal filaments (Lodge and Asbury 1988), fine roots (Lodge et al. 1991) and mesofauna (Zou and González 1997). The increase in litterfall over time likely will lead to a reduction in soil and litterfall losses (Larsen et al. 1999) as successional processes begin to stabilize the slopes (Walker et al. 1996; McDonald et al. 2002; Nicolau 2002).

Most C was found in landslide soils (<1% in plants on our young landslides), yet due to the high rates of erosion, up to one fourth of that C moves down slope each year on these young landslides. Because the landslides had such little vegetation cover, annual C inputs in litter were four to five times the standing C stocks in plant biomass (root and shoot combined). Litter outputs were also high, constituting approximately two times the C standing stocks during the first year of landslide succession. This relatively high flux of C is indicative of the highly unstable conditions found on landslides and other steep surfaces (Crozier 1986; Walker and del Moral 2003).

Plant responses also varied between soil types, with more shoot biomass on volcaniclastic soils and more root development on most of the dioritic soils. The very high C/N ratios reflected the relatively impoverished condition of these soils. Plants face two big hurdles in colonizing these landslides, instability and infertility (Walker et al. 1996). Both are ameliorated as vegetative cover increases. The more stable, more fertile (higher N, organic C, clay) volcaniclastic soils also supported the highest biomass and trees, shrubs and vines colonized volcaniclastic soils while herbs dominated dioritic soils (Shiels et al. 2008). These colonization patterns suggest that successional recovery on volcaniclastic soils will be more rapid than on dioritic soils.

On a landform scale, landslides can be considered as both erosional and depositional processes (Geertsema and Pojar 2007) where C moves down slope through a combination of actions (slumping, sliding, flowing or rafting of forest floor segments) that can be either slow or fast (Cruden and Varnes 1996). Landslides result in a down slope transfer of biomass and associated soil C (Scatena and Lugo 1995). The initial landslide scar is typically divided into three vertical zones, a slip face, a chute (where our plots were located) and a deposition zone (Guariguata 1990; Walker et al. 1996). In the slip face and chute, erosional processes predominate over depositional ones. In the deposition zone there can be deep burial of C from up slope plants and soils resulting in an irregular mixture of fertile and infertile soil (Adams and Sidle 1987). Much of the soil exported from landslides is washed quickly away in rivers (Pearce and Watson 1986), often accelerated by road maintenance activities (Shiels et al. 2008). All landslide zones are subject to further C inputs from up slope soil or plant sources, up slope or lateral litter transfer and in situ or lateral invasion by successional plant growth (Walker et al. 1996).

We present a conceptual model of pre- and post-landslide C dynamics on a hypothetical landslide (Fig. 3) in order to show the net loss from a given portion of the landscape, despite some additions as noted above, and the role of post-disturbance erosion and successional re-growth. Approximate C values, losses and rates of recovery in the first 30 years were derived from short-term studies (e.g., this study, Larsen et al. 1999) and two 52–56 year chronosequence studies (Guariguata 1990; Zarin and Johnson 1995b) as well as previous models (Pederson et al. 1992; Walker et al. 1996) and a global data base (e.g., Zinke et al. 1986). The final stage (150 years) is extrapolated from the same sources. Few soils are sampled below 1 m depth (Zinke et al. 1986), so the fluctuations of that pool (initially estimated as twice the <1 m deep pool due, in part, to previous landslide burial of soil C and/or soil profiles that are many meters deep) are largely speculative. However, even without the >1 m deep soil carbon estimates, our conclusions are the same—soil C erodes down slope and takes many decades to recover.

Our model represents an ideal average, but temporal dynamics on landslides are extremely heterogeneous (Shiels et al. 2006; Geertsema and Pojar 2007). For example, direct observations of LEF landslides during the past 20 year indicate that some initially bare landslide soils are now covered by 20 m tall trees while others still remain bare and eroding (L. Walker, unpublished data). Much of this variation could be due to initial carbon distribution and soil development. Despite inherent risks in extrapolating about longer-term landslide dynamics, predictive models are useful starting points for assessing landslide risks and determining the roles of soil C and plant succession in stabilizing eroding slopes (Cammeraat et al. 2007; Larsen 2008).

During landslide disturbance, all parts of the landslide except deeper soils in the deposition zone lose C down slope. The C in shallow soils (i.e., <1 m deep) in the deposition zone is diluted by low-C soils from up slope. The most rapid recovery is likely to occur aboveground and in shallow soils in the deposition zone, due to the newly buried, C-rich soils (Guariguata 1990). Litter inputs, surface soil erosion (as shown in this study) and rapid vegetative growth (Guariguata 1990; Walker et al. 1996) also are sources of C for this zone. The slowest recovery will probably occur in deep soils of the slip face and chute zones because these areas do not have the stability or

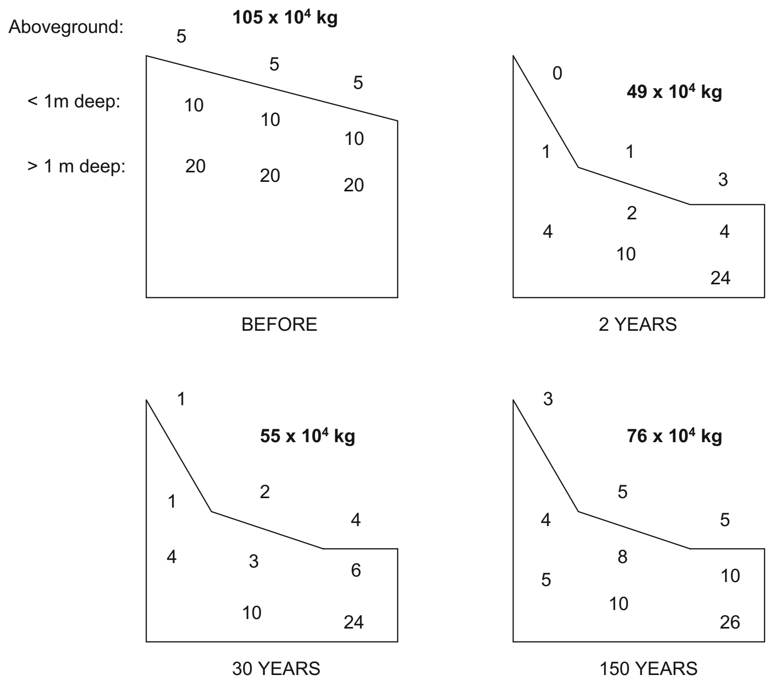

Fig. 3 A hypothetical model of how erosion from a landslide involving 1 ha of land moves C down slope in the LEF in northeastern Puerto Rico and how C values change over 150 years of post-landslide erosion and successional re-growth. The vertical rows of numbers (10^4 kg ha^{-1} C) represent (from *left to right*) the slipface, chute and deposition zones (and values at three strata: aboveground, <1 m soil depth, >1 m soil depth within each zone) on a cross section of a landslide. The *horizontal scale* represents a typical landslide length in the LEF that can vary between 30 and 1,000 m. *Bold values* are C sums for each 1 ha landslide. See text for more discussion

fertility to support plant growth and are isolated from surface inputs. For the entire landslide, we estimate that after an initial loss of approximately 50% of system C, only 60% of that loss will be recovered after 150 year. Our model therefore highlights that a given landslide patch is likely to represent, on average, a net loss of C for many decades after the initial event (despite potential areas within the landslide of rapid accumulation). This result contrasts with secondary succession following logging or agriculture where soil C may recover rapidly within a few decades (Lugo and Brown 1993). We have too little data to extrapolate further, but landslide soils might reach pre-disturbance levels (hypothetical in many highly disturbed landscapes; Walker and del Moral 2003) after 250 year (constant rate of accrual) to 500 year (declining rate; Zarin and Johnson 1995b). Of course, successional dynamics can be much slower, with little or no colonization on some landslides even after 20 year (Dalling 1995) or faster (with full recovery of both C and N within 40 year) as seen on Himalayan landslides (Pandey and Singh 1985; Reddy and Singh 1993).

Our results highlight that post-disturbance erosion can affect tropical landslides, even after the initial disturbance. When this occurs, landslides represent a net loss of C from the landscape. Soil type, rates of soil output and plant colonization dynamics are the principal factors determining recovery rates for C lost through landslides. Landslides therefore provide a long-lasting horizontal and vertical alteration of C.

Acknowledgements We thank Oscar Abelleira, Maria Aponte, Fred Landau, and especially Laura Weiss and Christine West for their pivotal roles in data collection. Lauren Kaminski and Bryan Necessary analyzed the soil and litter samples. Peter Bellingham, Matt Larsen, Carla Restrepo, Fred Scatena and Eduardo Velázquez provided helpful comments on an earlier draft. This research was funded by cooperative grants from the United States National Science Foundation (NSF), University of Puerto Rico, and the United States Forest Service, supporting the Luquillo Experimental Forest Long-Term Ecological Research Program (NSF grants: DEB-0218039, DEB-0620910).

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