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Landslides significantly alter land cover and the distribution of biomass: an example from the Ninole ridges of Hawai'i

Carla Restrepo[1,3,*], Peter Vitousek[1] and Paul Neville[2]
*[1]Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020, USA; [2]Earth Data Analysis Center, University of New Mexico, Albuquerque, NM 87131-6031, USA; [3]Current address: Department of Biology, The University of Puerto Rico, San Juan, Puerto Rico 00931–3360, USA; *Author for correspondence (e-mail: crestre@goliath.ennet.clu.edu; phone: +1 787 764 0000; fax: +1 787 764 2610)*

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Abstract

In the Ninole ridges of Hawai'i we investigated how landslides influence ecosystem development and modify land cover and the distribution of biomass. We estimated above and below-ground biomass, and N and P concentration in leaves (*Metrosideros polymorpha*) and very fine roots (all species), for vegetation developing on landslides of three age classes (young, < 18 yr; intermediate, ⩽ 42 yr; and old ca. 124 yr) and on undisturbed soils (ca. 430 yr). The undisturbed soils were derived from ash underlain by basalt. To quantify changes in land cover and the distribution of biomass we combined our estimates of biomass with estimates of the area covered by each vegetation class. The latter estimates were obtained from the analysis and classification of color-infrared aerial photographs. Average above- and below-ground biomass for the herbaceous vegetation (young landslides) was 10.4 and 3.2 t/ha, whereas for the ohia-non ash forest (intermediate and old landslides) was 37.5 and 5.2 t/ha, respectively. For the ohia-ash forest (undisturbed sites), average above and below-ground biomass was 354.6 and 9.5 t/ha, respectively. Average foliar N for the herbaceous and ohia-non ash forest ranged between 0.80–0.84%, whereas root P between 0.056–0.040%, respectively. For the ohia-ash forest, average foliar and root P was 0.918% and 0.036%, respectively. Based on changes in vegetation cover during the last 430 yr, we estimated rate of disturbance at 15% per century or equivalently that 53 t/ha biomass per century exited through the system. The removal of ash-derived soils by landslides significantly alters successional trajectories and by doing so may be transforming the Ninole ecosystems in irreversible ways.

Introduction

Landslides strongly influence forest ecosystems developing in humid tropical mountains. It has been estimated that rates of disturbance by landsliding vary between 0.1–20% per century (Gardwood et al. 1979; Spencer and Douglas 1985; Guariguata 1990; Scatena and Lugo 1995). As a consequence, an unestimated amount of biomass and soil organic matter is removed from these systems potentially impacting regional and global carbon budgets (Stallard 1998). In most studies it is assumed that biomass and soil organic matter will eventually reach pre-disturbance levels, however, rates of accumulation can be highly variable (Pandey and Singh 1984; Reddy and Singh 1993; Zarin and Johnson 1995a; Walker et al. 1996). Landslides remove nutrients in addition to biomass and soil organic matter (Lundgren 1978; Zarin and Johnson (1995a, 1995b)). These studies suggest that rates of nutrient accumulation are highly variable, potentially impacting rates of ecosystem development as it has been shown in agricultural landscapes affected by landslides (Douglas et al. 1986; DeRose et al. 1995).

The influence of landslides on humid tropical montane ecosystems goes beyond the slope scale. In fact, landslides redistribute biomass and nutrients between slopes and valleys leaving the mountain ridges almost intact. As a consequence, biomass of forests developing on slopes is generally lower than that of forests developing on mountain ridges. It has been suggested that the unstable conditions found on the slopes, and not the availability of nutrients, accounts for the observed differences: soils found on mountain slopes are relatively nutrient-rich (Burguess 1975; Silver et al. 1994; Scatena and Lugo 1995; Chen et al. 1997). Therefore, landslides are an important process structuring ecosystems at regional scales.

The islands of Hawaii are well known for their high erosion rates that result primarily from the activity of landslides (Wentworth 1943; Li 1988; Reid and Smith 1992; Keefer 1994; Hill et al. 1997). Surprisingly, little is known about the overall effect of landslides on Hawaiian ecosystems. Steep slopes become the dominant feature of old Hawaiian landscapes, and landslides may play an important role in ecosystem and landscape development. The only estimate available indicates that rate of disturbance by landsliding is 0.6% per century; this figure, however, is based on storm-triggered landslides (Wentworth 1943; Peterson et al. 1993). In addition to disturbing ecosystems developing on steep slopes, landslides may contribute to the overall diversity of geologic substrates and landforms, thus ecosystems, found in the islands. Tephra ejected from the volcanoes has buried basaltic substrates that may be subsequently exposed through the activity of landslides (Sato et al. 1973).

In this paper we evaluate the influence of landslides on a Hawaiian mesic to wet montane ecosystem. Specifically we ask: (1) how do biomass and (2) nutrient concentration of leaves and roots change over time after disturbance by landsliding, (3) what is the rate of disturbance by landsliding in an earthquake-prone environment, and (4) how does disturbance by landsliding translate into changes in land cover and the distribution of biomass. We conducted this work in the highly dissected Ninole ridges of Hawai'i for several reasons. First, knowledge of the age of the geologic substrates on the island of Hawai'i provides a means to estimate rates of ecosystem development (Raich et al. 1997; Aplet et al. 1998; Herbert and Fownes 1999; Ostertag 2001). In particular, comparing the Ninole ecosystems with those developing on the stable, undissected, substrates can help us understand differences between ecosystems developing on different landforms. Second, factors controlling ecosystem productivity, such as geological substrate, are relatively well understood for those ecosystems developing on the stable, undissected, substrates of the islands (Kitayama and Mueller-Dombois 1995; Kitayama et al. 1995; Raich et al. 1997; Vitousek and Farrington 1997). In particular, comparing the Ninole ecosystems with those developing on basalt and ash-derived soils may provide insights into those controlling productivity in ecosystems developing on steep terrain. Lastly, the Ninole ridges combine two geological substrates, ash and basalt, a feature found in many active mountains around the Pacific Rim. The removal of ash-derived soils by landsliding and the consequent exposure of basalt may account for important changes in ecosystem attributes over time.

Methods

Study site

We conducted this study in the Ninole ridges, a group of hills located in the SE portion of the island of Hawai'i (155°34′35″ W and 19°10′14″ N). Overall, the altitude of these ridges ranges from 480–1,116 m and that of our sampling sites at Puu One, Kaiholena, and Kaumaikeohu from 752–900 m (Figure 1, Table 1). The Ninole ridges are composed of tholeiitic basalt and represent remnants of the second oldest volcanic structure of the island (Hitchcock 1906; Stearns and Macdonald 1946; Lipman et al. 1990; Moore and Mark 1992; Wolfe and Morris 1996). Due to their old age they have some of the steepest terrain on the island. The ridges are surrounded by young (10,000 – 200 yr BP) valley-filling Mauna Loa lavas and thick weathered ash deposits (Lipman et al. 1990; Wolfe and Morris 1996).

Our sites have a mean annual temperature of 20 °C (based on a 5.8×10^{-3} °C/m lapse temperature rate) and mean total annual rainfall of 4,094 ± 1,099 mm (Atlas of Hawaii 1983; DNLR 1983). A climatological station that operated at the base of Kaiholena between 1964–1972 yielded a total annual average rainfall of 2,954 ± 586 mm (DNLR 1983). According to these data our sites can be classified as subtropical wet forest (Holdridge 1967) or montane mesic to wet forest (Loope 2000) dominated by ohia trees (*Metrosideros polymorpha*). Most of the hills comprising the Ninole system are within the Kau Forest Reserve. In part because of their relatively remoteness and steepness, and in part because of the high rainfall, the Ninole ridges where we conducted this study have been little influenced by present day human activities, including road construction, logging, and hunting.

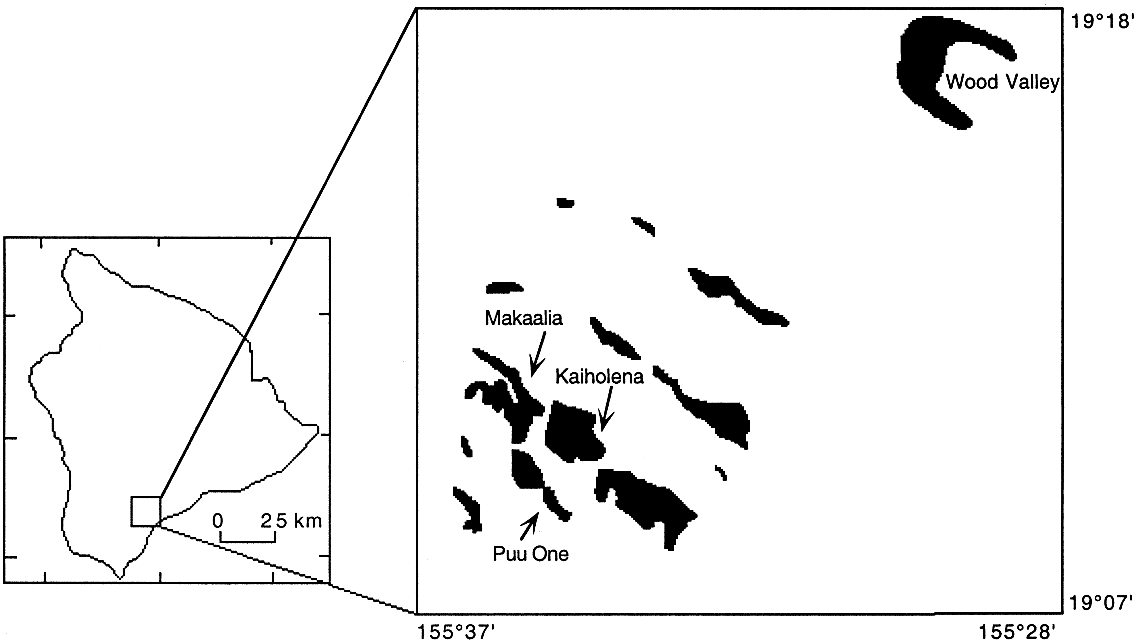

Figure 1. Location of the Ninole ridges in the Island of Hawai'i. Based on the Hawaii county, Hawaii, topographic county map series, USGS.

Table 1. Characteristics of the landslides sampled in this study. The angle of the slide plane was 40° and the chute of the landslides exceeded 100 m in most instances.

Age class	Age yr	Dating method[1]	Site	Ninole ridge	Altitude m
Young	< 18	1978-no/1992-yes	L7	Kaumaikeohu	~ 700
Young	< 18	1978-no/1992-yes	L1	Kaiholena	888
Young	< 4	1992-no	L5	Kaiholena	794
Intermediate	< 42	1954-no/1965-yes	L8	Puu One	~ 844
Intermediate	< 42	1954-no/1965-yes	L9	Puu One	~ 844
Intermediate	42	1954 (fresh scar)	L6	Kaiholena	812
Old	< 124	< 1954[2]	C1	Kaiholena	~ 876
Old	< 124	< 1954[2]	L2	Kaiholena	888
Old	< 124	< 1954[2]	L4	Kaiholena	762
Undisturbed	430	charcoal[3]	C2	Kaiholena	750
Undisturbed	430	charcoal[3]	C3	Puu One	~ 860
Undisturbed	430	physiognomy	C4	Puu One	~ 829

Landslide age was determined by examining
[1]aerial photographs taken between 1954–1992,
[2]historical earthquake records, and
[3]C-14 dating charcoal remains (see Methods).

Soils of the Ninole hills have been classified as rough broken, to describe the fact that they are found on steep terrain, where stones and rock outcrops are common (Sato et al. 1973). A soil pit dug at Kaiholena under closed *Metrosideros polymorpha* forest, however, showed a well-developed soil (Table 2). The soils, derived from volcanic ash underlain by basalt, are shallow (35 cm in depth until reaching the hard basalt), and have been classified as hydrous, perrihydritic, isothermic Lithic Hydrudands (R. Gavenda, *unpublished data*). Soils from the head cut area of landslides are shallower and represent a mixture of organic matter and variable amounts of soil from different horizons.

Table 2. Soil profile of undisturbed soil in Kaiholena Ridge (site C2; 750 m), Hawai'i (R. Gavenda and K Harrington, *unpublished data*, USDA/NRCS, Hilo-Hawaii). These soils have been classified as hydrous, perrihydritic, isothermic Lithic Hydrudands. Soils from the landslides represent a mixture of organic matter and variable amounts of soil from different horizons.

Horizon	Depth cm	Color[1]	Texture[2]	pH[3]	Observations
A	0–2	Black (10 YR 2/1)	Loam	4.2	
Bw	2–8	Black (10 YR 2/1)	Clay loam	6.2	Ash
2A	8–18	Black (10 YR 2/1)	Clay loam	6.2	
2Bw	18–29	Dark brown (7.5 YR 3/2)	Sandy loam	6.6	Ash
3A	29–34	Black (10 YR 2/1)	Clay loam	6.6	Charcoal remains
4R	34	Light olive brown (2.5 Y 5/3) and reddish brown (5YR 6/4)			Basalt, 1 cm weathering rind

[1] Determined in moist samples
[2] Apparent field texture
[3] Measured with organic dyes

Sampling procedure

We sampled vegetation developing on landslides of three different ages (young, 4–17 yr; intermediate, 18–42 yr; and old, ca. 124 yr) plus undisturbed sites (ca. 430 yr). The approximate age of these landslides and undisturbed forest at Puu One, Kaiholena, and Kaumaikeohu was established by using aerial photographs taken in 1954, 1965, 1978, and 1992, by using historical earthquake records, and by dating charcoal remains (Table 1). Landslides in the Ninole ridges are classified as planar debris slides: they exhibit a definable shear surface at the basalt/ash-derived soil interface (Varnes 1958; Thomas 1994).

Fresh landslide scars on the aerial photographs were assigned a maximum age that represented the time elapsed since the photograph was taken. The photographs allowed us to identify the young and intermediate landslides. Revegetated landslide scars on the 1954 aerial photographs resembling those triggered by earthquakes (Harp et al. 1981) were classified as old. In 1868, the largest earthquake ever recorded in Hawai'i (magnitude > 7.2 in the Richter scale) caused widespread landsliding in Wood Valley, the northernmost hill comprising the Ninole ridge system (Lipman and Swenson 1984; Wyss and Koyanagi 1992). We are assuming that the landslides seen on the 1954 aerial photographs were created during or after this event, giving them a maximum age of 124 yr.

Forests developing on undisturbed soils were dated based on the age of charcoal remains. We found abundant charcoal in the deepest A horizon which was overlain by an ash-derived soil horizon that had a characteristic yellowish color and did not have any evidence of carbonizing vegetable matter (2Bw; Table 2). Charcoal recovered from Kaiholena (n = 2 sites, including the soil pit) and Puu One (n = 1) was C-14 dated at 325 ± 100 yr BP, 260 ± 90 yr BP, 525 ± 60 yr BP, respectively (Laboratory of Isotope Geochemistry, The University of Arizona; conventional dates ± 1 SD). Part of the variation in the above dates may represent a sampling artifact. Our charcoal samples were not sorted for small roots and twigs; it is well known that larger roots and twigs can introduce erroneously old ages reflecting the age of the trees at the time they were burned (Clague et al. 1999). Based on the charcoal remains, we estimate that the forest was burned 370 yr BP or that the undisturbed forest is ca. 430 yr old.

The stratigraphic position of the charcoal and its widespread distribution suggests that a large fire burned the forest and that the remains were subsequently covered by ash. We postulate that the forest that developed afterwards is represented by our ohia-ash forest (see below), and that it became the dominant vegetation of the Ninole slopes until 1868, the year in which a strong earthquake hit this part of the island. The fire that destroyed the forests developing on the Ninole ridges may have resulted from young lava flows banking against the ridges (Lipman and Swenson 1984) or a major drought that impacted Mauna Loa ca. 400 yr BP (J. Lockwood, personal communication). The ash from which the 2Bw and Bw horizon were derived may represent reworked Pahala ash (P. W. Lipman, personal communication) and Keanakako'i ash produced by Kilauea ca. 1790 AD (Swanson et al. 1998), respectively.

We sampled three landslides per age category and three undisturbed forest sites. In the head cut or point of initiation of each landslide we delimited a 20 × 15-m plot perpendicular to the contour lines, with the 20-m axes parallel and adjacent to the landslide edges. In the undisturbed forest sites the plots were placed at random but always with the longest axis perpendicular to the contour lines. The 300 m^2 plots were further subdivided into twelve-25 m^2 subplots, 8 located at the edge and 4 at the center of the landslides. We randomly selected two edge and two center subplots per plot (total of 100 m^2) to sample the above-ground and below-ground vegetation at each landslide and undisturbed site. Sampling of the vegetation took place between August 1996–August 1997. Woody plants with dbh ⩾ 2.8 cm (trees, treelets) were sampled in each of four 25 m^2 subplots; woody plants with dbh < 2.8 cm (saplings, shrubs) and herbaceous plants (grasses, sedges, forbs, orchids, vines, rhizomatous forbs) were subsampled in each of four 2.25 m^2 quadrats within the 25 m^2 subplots. We counted, identified to species level, measured diameters (stems ⩾ 2.8 and < 2.8 cm at 1.3 m and 0.2 m above ground, respectively), and visually estimated the heights of all individuals. For herbaceous plants we estimated percentage cover, as the proportion of ground covered by each species within the quadrats.

Several assumptions underlie the use of chronosequences to evaluate ecosystem changes over time (Foster and Tilman 2000). Two key assumptions are that all sites have been affected by the same climate and disturbance regime and that they have been influenced by the same pool of species. Given the temporal (500 yr) and spatial (80 km^2) extent of this study, we know that all sites have experienced the same climate, including the occurrence of tropical storms that may trigger landslides. The Ninole ridges have been influenced by the same pool of species, yet in recent years there has been an increasing influence of alien species (Restrepo and Vitousek 2001).

Biomass

Above-ground biomass of shrubs and trees for each subplot was estimated using allometric equations that included tree height and dbh as predictors of biomass (Aplet and Vitousek 1994; Raich et al. 1997; Aplet et al. 1998). Above-ground biomass of herbaceous plants was estimated in young landslides by harvesting and weighing all herbs in one of the four 2.25 m^2 quadrats per subplot per plot. A subsample of the harvested plants was weighed, oven-dried at 70 °C for > 24 h, and weighed again to obtain a fresh to dry weight conversion factor used to calculate the biomass for the entire quadrat. Our calculations of above-ground biomass may underestimate the real values because we did not include tree ferns; in the islands of Hawaii tree fern biomass represents a small proportion of total tree biomass (0.13 ± 0.07) (Kitayama et al. 1997). At our sites we could not measure stem length because most tree ferns had prostrated stems with the distal portion perpendicular and often a meter or more above the ground; stem length is the predictor of tree fern biomass in the allometric equations developed by Aplet and Vitousek (Aplet and Vitousek 1994).

Below-ground biomass for each subplot was estimated by collecting soil at each of the four corners of the 25 m^2 subplots. Soil samples were obtained using a 5.1 cm diameter corer and were collected at depth increments of 5 cm until reaching the hard basalt (range of depths, 1–25 cm; average soil depth for young, intermediate, old landslides, and undisturbed forest 8.4, 11.1, 13.0, and 12.7 cm). Each soil sample was divided in half and the two subsamples were frozen until processed. One of the subsamples was processed within 1–2 weeks: after thawing, the soil was weighed and washed through a 0.5 mm mesh soil sieve. We classified the roots by size (< 1.0, very fine; 1.0– < 2, fine; 2– < 5, small, and ⩾ 5, coarse, mm diameter) and condition (alive and dead) after which we dried (70 °C for > 24 h) and weighed them. To standardize our estimates of root biomass we added the values for the first three depth increments (15 cm) per corner per subplot. This yielded a value for root biomass for the first 15 cm of soil.

Foliar and fine root nutrients

In the islands of Hawai'i foliar and very fine root N and P concentration vary across sites and this variation has largely been explained by differences in nutrient availability (Vitousek et al. (1988, 1992, 1995)). Moreover, changes in foliar and very fine root N and P in response to fertilization indicate that these variables can be informative about limits to ecosystem productivity in Hawaiian sites. In order to infer changes in nutrient status resulting from disturbance by landsliding we measured N and P concentrations both in leaves (*Metrosideros polymorpha*) and very fine roots (all species combined). We collected mature sun leaves from five *Metrosideros polymorpha* individuals (glabrous variety) growing on each landslide and undisturbed forest site. All root samples (dry live very fine roots) per subplot were pooled to obtain a composite sample per subplot per landslide. Dry leaves, as well as dry live very fine roots, were ground to pass through a 0.5 mm mesh sieve. Leaves and roots were digested and analyzed to determine total phosphorous and nitrogen concentrations (expressed as %) following standard procedures (Vitousek et al. (1988, 1992, 1995)).

Changes in land cover and biomass

To establish the extent to which landslides have affected mesic to wet montane ecosystems developing on the Ninole ridges (Kaiholena, Makaalia, Puu One) we digitally processed three color-infrared aerial photographs taken in 1992 (HI54 27-1, 27-2, and 26-3; scale 1:12,000). A similar procedure was used with remotely sensed data to map landslides in Papua New Guinea (Greenbaum et al. 1995). This method has several advantages over the traditional method of examining aerial photographs stereoscopically. First, the images can be analyzed faster and more objectively. After selecting a sample of pixels that represent well-known classes identified with help from other sources, such as ground-truthing, the computer is "trained" to identify pixels with similar characteristics. Second, the delimitation of clusters belonging to a given class and subsequent mapping is more accurate. Once the pixels are classified they are resampled to obtain clusters that are already projected onto a plane that conforms to a chosen map projection (ERDAS 1997; Schott 1997).

The photos were scanned at 1,000 dpi creating a three band digital file with separate image bands representing the visible green, visible red, and near-infrared wavelengths. The photos were ortho-rectified (the Punaluu, HI, 7′5 series quadrangle served as the base map and the USGS digital elevation model as the topographic source), projected into UTM (Zone 5, Datum NAD27, Spheroid Clark 1866, with a 1 × 1 m resolution), and mosaic. Air photos from areas of high relief have a number of radiometric problems associated with them, including differential illumination angles and different reflectance responses between and within photos, respectively. As a result, a traditional spectral-based classification procedure was not considered viable. Instead we created a Normalized Difference Vegetation Index (NDVI) image to enhance the greenness reflectance differences and texture images to emphasize variability in the neighborhood around the pixels. The NDVI, as a ratio of the near infrared over the visible red, diminishes the differential illumination effect within and between photos by emphasizing the contrast difference between the two bands on a pixel by pixel basis. The texture images were generated for the visible red and green bands to enhance characteristics such as heterogeneous vs. homogeneous cover type, stand height, and crown size. The NDVI and texture images were combined and used subsequently in the classification.

We defined four vegetation classes based on the physignomy (Jacobi 1978) and presence of ash-derived soils (C. Restrepo, unpublished data). These classes are: herbaceous vegetation (vegetation developing on young landslides), open ohia-non-ash forest (ohia forest developing on the intermediate and old landslides; crown cover > 15–60%), open ohia-ash forest (ohia forest with short trees; crown cover < 15%), and closed ohia-ash forest (ohia forest with tall trees developing on the undisturbed sites; crown cover > 60%). For each of the four classes we gathered at least two spectral signatures that were obtained from sites that we had sampled, visited, or recognized on the aerial photographs as belonging to a given class. We used the maximum likelihood method to classify the pixels and generated a vegetation map for the Ninole ridges. We used ERDAS Imagine v8.3 to process and analyze the digitized aerial photographs (ERDAS 1997).

Rate of disturbance by landslides, RD, was estimated as:

$$RD = [DA/TA]*1/T,$$

where DA = area denuded by landslides, TA = total slope area, and T = time between observations (Gardwood et al. 1979); traditionally it is expressed as proportion of area denuded per century.

To calculate changes in the distribution of biomass resulting from the activity of landslides we estimated the contribution of each vegetation class to the total biomass. We did so by multiplying the total area of each vegetation class by its corresponding average biomass.

Results

Above- and belowground biomass

Above-ground biomass differed significantly among the landslide-age categories and the undisturbed forest (ANOVA, $F_{3,8} = 19.84$, $P = 0.0005$, Table 3); it was smaller in young and intermediate than in old landslides and the undisturbed forest (Figure 2). Alien species, represented mostly by grasses, orchids, and rhizomatous plants were present in all landslide-age categories, but in young landslides they were the dominant life form and made a substantial contribution to the estimates of above-ground biomass (alien species contributed 83% of the above-ground biomass in young landslides). When we excluded the alien species from the analysis, the differences shown above became more pronounced (Figure 2, Table 3).

Below-ground biomass differed significantly among the landslide-age categories and the undisturbed forest when considering very fine and fine (< 2 mm) and coarse ($\geqslant$ 5 mm) roots (ANOVA, $F_{3,8} = 4.79$, $P = 0.03$ and $F_{3,8} = 6.22$, $P = 0.02$, respectively; Table 3). Very fine and fine root biomass was smaller in young, intermediate, and old landslides than in the undisturbed forest (Figure 2). Coarse root ($\geqslant$ 5 mm diameter) biomass was smaller in young than in intermediate and old landslides, and the undisturbed forest (Figure 2).

Root and foliar nutrients

Foliar N but not foliar P differed significantly among the three landslide-age categories and the undisturbed forest. Foliar N was highest in leaves of *Metrosideros polymorpha* individuals growing on old landslides and the undisturbed forest (Kruskal Wallis test, H = 16.84, df = 3, $P < 0.001$ and H = 3.37, df = 3, $P < 0.2$, respectively; Figure 3). In contrast, the concentration of P (%) but not of N (%) in very fine roots differed among the landslides and undisturbed forest. P was highest in root samples collected from young and intermediate landslides (K-W, H = 11.25, df = 3, $P < 0.01$ and H = 3.43, df = 3, $P < 0.3$, respectively; Figure 3).

Changes in land cover and biomass

The slopes of Kaiholena, Makaalia, and PuuOne comprise 393 ha. Presently, 86 ha are covered by closed ohia-ash forest, 52 by open ohia-ash forest, 165 by

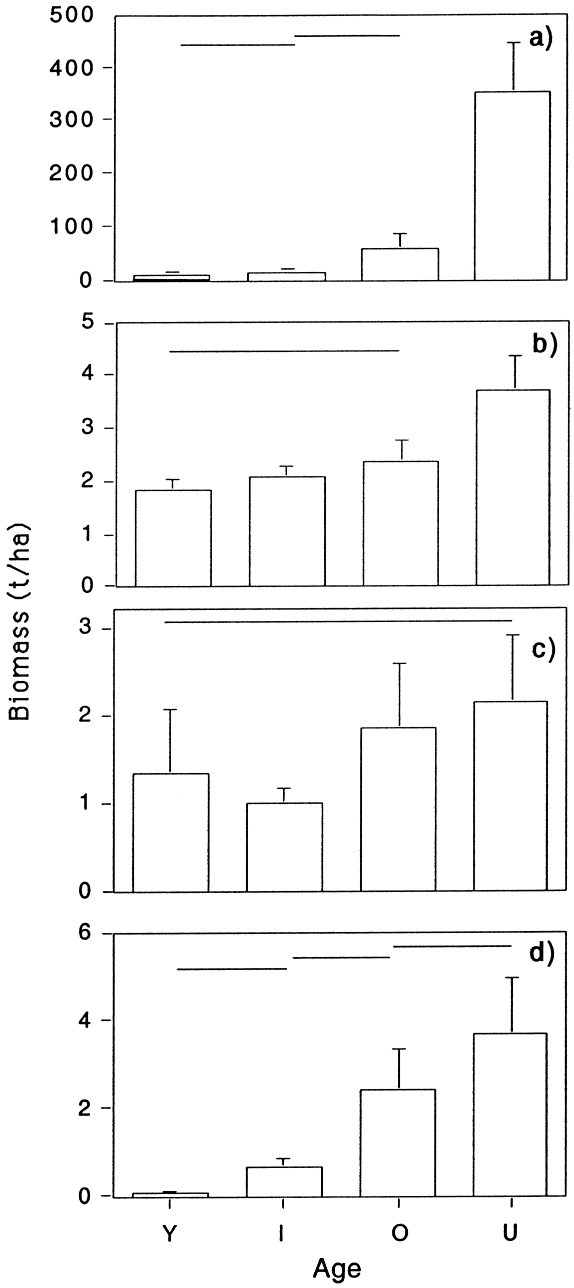

Figure 2. Above- and below-ground biomass (t/ha) for the three landslide-age categories and undisturbed forest in the Ninole ridges of Hawai'i. (a) Above-ground, (b) below-ground biomass of very fine to fine roots (< 2 mm diameter), (c) small roots (2–5 mm diameter), and (d) coarse roots (> 5 mm diameter). Black line in young landslides (a) corresponds to the contribution of native species to above-ground biomass. Bars overlain by the same line were not significantly different at an alpha of 5% using a post-hoc Games-Howell multiple comparison test on log-transformed data. Values represent means ± 1SE.

Table 3. Results of five one-factor ANOVA's for above- and below-ground biomass in Hawaiian landslides. (°) based on log-transformed data.

Effect		Above-ground biomass°				Below-ground biomass					
		Alien + Natives Species°		Native Species°		Very fine and fine roots°		Small roots		Coarse roots°	
	df	MS	F	MS	F	MS	F	MS	F	MS	F
AGE	3	2.72	40.32**	1.39	19.84**	0.05	4.78*	0.79	0.57	0.22	6.22*
Error [Site (Age)]	8	0.07		0.07		0.01		1.39		0.04	

(*) $P < 0.05$, (**) $P < 0.01$.

Table 4. Extent of vegetation classes in the Ninole ridges of Hawai'i (only includes Kaiholena, Makaalia, and PuuOne) based on the analysis of infrared aerial photographs. AG: above-ground and BG: below ground biomass. We excluded from our analyses the areas comprising the flat substrates on top of Kaiholena and Makaalia and a total of 22.4 ha corresponding to heavily shadowed areas.

Vegetation Class	AGB t/ha mean ± 1SE	BGB t/ha mean ± 1 SE	Area in 1992 ha	Total Biomass in 1992 t	Total Biomass in 1868 t
Herbaceous	10.4 ± 1.8	3.2 ± 0.8	90.1	1,225	
Ohia, open non-ash	37.5 ± 16.3	5.2 ± 1.1	165.1	7,050	
Ohia, open ash	218.8[1]	9.2[1]	51.6	11,765	11,765
Ohia, closed ash	354.6 ± 93.5	9.6 ± 2.5	86.2	31,399	124,321[2]
Total			393.0	51,439	136,086[2]

[1] We used the lowest value of biomass obtained for the ohia, closed ash forest.
[2] Prior to 1868 earthquake the Ninole ridges were likely to be dominated by the closed ohia-ash forest; we used the average value of biomass obtained for the closed ohia-ash forest.

open ohia-non-ash forest, and 90 ha by herbaceous vegetation (Table 4). The area influenced by landslides includes that where the herbaceous vegetation and the ohia non-ash forest are found. To estimate rates of disturbance by landsliding in the Ninole ridges we used two values of T, the time between observations. The first, a conservative figure of 430 yr, assumes that landslides started to affect the Ninole slopes some time after the forest was burned and gives a disturbance rate at 15% per century. The second, a liberal figure of 124 yr, assumes that the 1868 earthquake was responsible for most of the changes observed today and gives a disturbance rate at 51% per century. In both instances estimates are maximum because we assume that landsliding (vs. sheet erosion) has been the main processes denuding the Ninole slopes.

Combining the average biomass with the area covered by each vegetation class we estimated that landslides have contributed to the net removal of 84,685 t biomass over the past 430 years, or equivalently to 50 t/ha per century (Table 4). Prior to the 1868 earthquake the Ninole system was dominated by the ohia-ash forest and potentially sustained 136,086 t of biomass. The current distribution of vegetation classes indicates that 255 ha of the ohia-ash forest, or equivalently 92,930 t of biomass, has been removed since the time of the earthquake. During the last 124 yr, the areas affected by landslides (open ohia-non-ash forest and herbaceous cover) have accumulated 8,245 t of biomass.

Discussion

Differences in biomass and foliar and root nutrients between landslides and the undisturbed forest suggest that the time required to reach predisturbance levels exceeds the 124 yr of our old landslides. Alternatively, it suggests that ecosystems developing on landslide-disturbed areas effectively differ from those developing on ash-derived soils, never reaching predisturbance levels. Furthermore, differences in biomass and foliar and root nutrients between the Ninole substrates (steep, unstable substrates) and those of equivalent age since time of exposure elsewhere in Hawai'i (shallow, stable substrates), suggest that geomorphic setting can account for some of the observed results.

Table 5. Above- and below-ground biomass (t/ha), N and P concentrations in leaves of *Metrosideros polymorpha* (glabrous variety) and roots (all species) for selected sites on two different substrate types in the island of Hawai'i. All these sites correspond to mesic and wet montane ecosystems receiving ⩾ 2500 mm and located 900–1200 m above sea level. Mean (1SE). HAVO, Hawai'i National Park.

Biomass	Ash			Basalt		
	Ninole 425 y	Thurston-HAVO 300 y	Laupahoehoe 20,000 y	Ninole 130 y	Lava-flow 130 y	Lava-flow 3400 y
AGB	354.1[1] (93.5)	177.6[8] (21.0)	266.6[8]	59.4 (28.8)	16.4[4] (1.5)	129.5[4] (21.5)
BGB (fine roots)	3.7[1] (0.6)	2.5[2,6*]	3.6[6,9]	2.4[1] (0.4)		
%N leaves	0.947[1] (0.039)	0.740[7] (0.040)	1.170[7] (0.030)	0.836[1] (0.018)	0.630[7] (0.010)	0.800[3] (0.040)
%P leaves	0.062[1] (0.003)	0.062[7] (0.003)	0.090[7] (0.003)	0.065[1] (0.003)	0.047[7] (0.002)	0.057[3] (0.003)
%N roots	0.946[1] (0.061)	0.873[6,8] (0.052)	0.768[6,8] (0.084)	1.027[1] (0.075)		
%P roots	0.038[1] (0.003)	0.042[6,8] (0.0013)	0.055[6,8] (0.008)	0.042[1] (0.003)		

[1]this study, [2]Gower and Vitousek (1989), [3]Vitousek et al. (1992), [4]Raich et al. (1997), [5]Aplet et al. (1998), [6](Ostertag 2001), [7]Vitousek (1998), [8]Herbert and Fownes (1999). [*] this value represents the average of three studies that have estimated fine root biomass in or close to the control plots of a fertilization experiment at Thurston-HAVO

Ecosystem productivity and landslides

To distinguish between the two hypotheses presented above we compared the observed biomass for the 124-yr old landslides with that expected for an ash substrate of the same age in the island of Hawai'i. Using biomass data from forest stands developing on ash-derived soils (Kitayama et al. 1995) and assuming that biomass accumulates according to a logistic growth model, we estimated that biomass in a 124-yr-old ash substrate should be 268 t/ha. This figure is higher than the 59.4 t/ha (above- and below-ground biomass) reported for the 124-yr-old landslides (Figure 2, Table 5) and strongly suggests that biomass accumulation is slower in landslide-disturbed areas. Substrate characteristics, basalt versus ash, or the continuous removal of the vegetation and soil may largely explain these differences; we are inclined towards the first explanation. Elsewhere in Hawai'i, ecosystems developing on shallow, stable substrates of similar age and climate but different geology ('a'a and pahoehoe lava versus ash) vary: those developing on lava not only exhibit lower values of biomass than those on ash but accumulate biomass at slower rates (Kitayama et al. 1995). Even though lava and ash have a similar chemical composition they have a very different texture, a feature that strongly influences the movement of water and therefore weathering rates.

Values of above- and below-ground biomass obtained for the Ninole ridges are higher than those reported for equivalent substrates elsewhere in the island of Hawai'i (Table 5). These other substrates, unlike those of the Ninole ridges, represent primary undissected substrates that were not weathered or disturbed before they were colonized by plants. Above-ground biomass of our 124-yr-old landslides was higher than that of lava flows of similar age; however, it was similar to that of a 3,400-yr-old lava flow (Table 5). Also, above-ground and below-ground (very fine and fine roots) biomass in the 430-yr-old Ninole ash-forests were greater than those of forest developing on a 300 yr ash-derived soil but similar to those of a forest developing on a 20,000 yr ash-derived soil (Table 5). These differences suggest that rates of biomass accumulation on both basalt and ash-derived soils may be faster in the Ninole ridges than in equivalent substrates on the island of Hawai'i. The lowering of the soil profile due to erosion processes operating on steep slopes may explain these results. It is well known that weathering rates, and thus the release of nutrients, decrease as the depth of the soil profile increases (Selby 1993; Thomas 1994). Thefore, lowering of the soil profile may contribute to the rejuvenation of soil.

Data on foliar and very fine root P and N concentration provide further support to the idea that landslides influence the productivity of Hawaiian montane ecosystems. Concentration of P in very fine roots was highest in young landslides and decreased in old landslides and the undisturbed forest whereas concentration of N in leaves of *Metrosideros polymorpha* was highest in the undisturbed forest and decreased in intermediate and young landslides (Figure 3). Two explanations may account for the patterns observed in roots. First, high values of P in young landslides may reflect variation in species composition. Landslides in the Ninole ridges are presently colonized by alien species that are highly mycorrhizal (Koske et al. 1992) and a high concentration of P in very fine roots may reflect this fact. Second, a high concentration of P in roots may reflect the availability of P as suggested by the low K/P ratios reported for the Ninole basalts (Lipman et al. 1990). In fact, after thousands of years of weathering, little mobile elements like P may become available through the mechanical activity of roots and the occurrence of landslides. Whereas roots break and expose fresh basalt as evidenced by the presence of rocks within the root mats of uprooted trees, landslides remove ash, and in many instances basalt, over large areas. Finally, a mixture of soils derived from ash and basalt during the formation of landslides may result in an increase in soil P: volcanic ash weathers faster than basalt and P may become available to plants.

Results for leaves may reflect the availability of N. Studies conducted elsewhere in Hawaii have shown that foliar N is highest at the Laupahoehoe forest (1.170%; Table 5), the most productive site of several that have been intensively studied (Vitousek and Farrington 1997; Vitousek 1998). Foliar N from the Ninole ohia-ash forest (0.947%, Table 5) is very close to that reported for Laupahoehoe. We emphasize changes in P and N, since they have been shown to limit ecosystem productivity of Hawaiian mesic ecosystems (Vitousek et al. 1993; Vitousek and Farrington 1997).

Changes in land cover and biomass

The presence of ash-derived soils underlying the undisturbed forest provided a signature that allowed the recognition of what may be considered two different ecosystem states in the Ninole ridges: one characterized by basalt- and the other by ash-derived soils. Differences between these two ecosystem types, in combination with known dates at which the ohia-ash forest established, indicate that disturbance by landslides has significantly influenced the Ninole ecosystems within the last 430 yr (Table 4).

Rates of disturbance by landsliding for the Ninole ridges were estimated at 15% per century (with a maximum value of 51%). These figures are higher from those estimated for Oahu (0.6–1.7%) and Hawai'i (4%). The value for Oahu is based on an inventory of storm-triggered landslides covering a period of 59 years (Peterson et al. 1993). The value for Hawai'i is based on erosion rates estimated from seismic-moment release and volume of earthquake-induced landslides (Keefer 1994). Elsewhere in the tropics, rates of disturbance by landsliding have been estimated at 3% and 14% for storm and earthquake-triggered landslides, respectively (Spencer and Douglas 1985). For earthquake-triggered landslides (earthquake magnitude 6.0–7.0) the range is 5–30%. Our figure of 15% is within the range of earthquake-induced landslides; our figure of 51%, although outside the range may well indicate that the epicenter of the 1868 earthquake was in the vicinity of the Ninole ridges. It has been shown that close to the epicenter of earthquakes, denudation by landslides is up to 60% of the area (Nieto et al. 1991; Mora and Mora 1994).

Changes in land cover have had a profound impact on the Ninole ecosystems, which have seen an overall decline in biomass due to the loss of the ash-derived soils and the forest developing on them. In addition, we have shown elsewhere that these changes have been accompanied by changes in species composition (Restrepo and Vitousek 2001). In particular, young landslides are being colonized by alien species, mostly grasses and orchids that are affecting the establishment of native species and the growth of the dominant tree species in these forests, *Metrosideros polymorpha*. In many active mountain belts around the world it is common to find a combination of two geological substrates, ash and basalt, as it is observed in the Ninole ridges. We suspect that in these regions landslides may also be significantly altering successional trajectories, therefore transforming ecosystems in irreversible ways.

Landslides not only are transforming the Ninole ecosystems by changing the substrate upon which they develop but also are altering carbon fluxes in important ways. Combining our disturbance rate of 15% per century with the average biomass for the ohia-ash forest, we estimate that 53 ± 14 t/ha (mean ± 1SE) of biomass per century is leaving the system. In areas with well-developed fluvial systems (not the case in the area comprising the Ninole ridges), a large proportion of the organic carbon contained in the biomass and soil removed by landslides is transported into the channels. Eventually this organic carbon will be sequestered in alluvial plains and the continental shelves (Stallard 1998). Likewise, additional atmospheric CO_2 will be sequestered by the vegetation developing on the denuded slopes at rates that will largely depend on the productivity of the sites. In this sense, wet tropical mountains may be playing an important role in the carbon cycle, both regionally and globally.

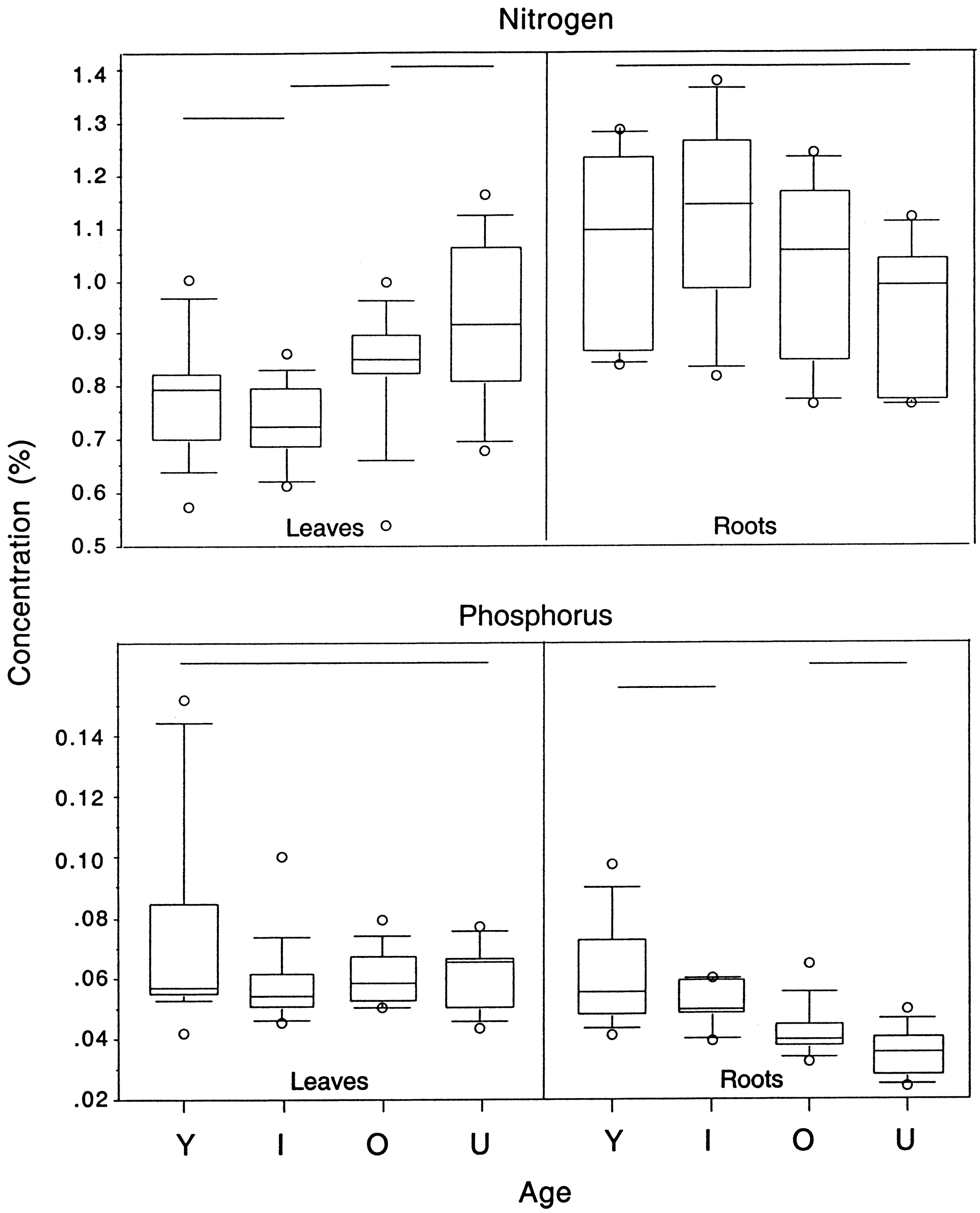

Figure 3. Box plots for nitrogen and phosphorus concentration (%) in leaves of *Metrosideros polymorpha* and very fine roots (< 1 mm diameter) for the three landslide-age categories and the undisturbed forest in the Ninole ridges of Hawai'i. Bars overlain by the same line were not significantly different at an alpha of 5% using a non-parametric multiple comparison test.

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