

## PERSISTENCE OF ROCK-DERIVED NUTRIENTS IN THE WET TROPICAL FORESTS OF LA SELVA, COSTA RICA

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**Abstract.** We used strontium isotopes and analysis of foliar and soil nutrients to test whether erosion can rejuvenate the supply of rock-derived nutrients in the lowland tropical rain forest of La Selva, Costa Rica. We expected that these nutrients would be depleted from soils on stable surfaces, a result of over one million years of weathering in situ. In fact, trees and palms in all landscape positions derive a relatively high percentage ( $\geq 40\%$ ) of their strontium from bedrock, rather than atmospheric, sources. The fraction that is rock-derived increases on slopes, but with no detectable effect on plant macronutrient concentrations. These results differ from those in a similar ecosystem on Kauai, Hawaii, where plants on uneroded surfaces derive almost all of their foliar Sr from atmospheric, rather than bedrock, sources. The results from La Selva challenge the assumption that tropical Oxisols in general have low nutrient inputs from bedrock, and support the hypothesis that erosion can increase the supply of these nutrients in lower landscape positions.

**Key words:** bedrock weathering; Costa Rica; erosion; foliar nutrients; Hawaii; La Selva; *Metrosideros polymorpha*; nutrient derivation; Oxisols; *Pentaclethra macroloba*; strontium; tropical rain forest.

### INTRODUCTION

Ecosystems on tropical Oxisols are widely believed to be depleted in phosphorus (P) and other putatively rock-derived nutrients. Walker and Syers (1976) provided a theoretical framework that predicts the occlusion and loss of soil phosphorus during ecosystem development. Observations on an age sequence of sites across the Hawaiian Islands demonstrate that element inputs via rock weathering decline to very low levels in the oldest sites (Chadwick et al. 1999, Vitousek 2004), and that P availability is low and P supply limits plant production on an old tropical Oxisol on the island of Kauai (Crews et al. 1995, Herbert and Fownes 1995). Moreover, measurements of strontium (Sr) isotopes confirm that atmospheric deposition of marine aerosol replaces weathering as the primary source of cations in older Hawaiian sites (Kennedy et al. 1998, Vitousek 2004).

Nevertheless, it is unclear how generalizable these patterns are within and among tropical landscapes. Most chronosequence studies carefully limit their analyses to geomorphically stable, minimally eroded surfaces (Walker and Syers 1976, Vitousek 2004, Wardle et al. 2004), but many tropical landscapes are actively eroding, and erosion on older landforms in the Hawaiian Islands increases the availability of rock-derived nutrients in lower landscape positions to the point

at which these elements are not in short supply (Vitousek et al. 2003, Porder et al. 2005a). The fraction of Sr derived from weathering increases on eroded slopes of older landscapes, as does the availability of P in soils and foliar P concentrations (Porder et al. 2005b).

Like the older soils in Hawaii, many continental Oxisols have small pools of available P and other putatively rock-derived elements (Sanchez 1976, Cuevas and Medina 1988, Tanner et al. 1998). We asked whether inputs of rock-derived nutrients are indeed low on uneroded surfaces, and if erosion increases the supply and/or availability of rock-derived nutrients on slopes in the lowland tropical rain forests of La Selva Biological Station, Costa Rica. La Selva supports deep, volcanically derived Oxisols and substantial local topography, and thus provides a useful test of the generality of processes that have been documented on old, volcanically derived soils in Hawaii.

### METHODS

#### *Site description*

La Selva Biological Station is in the Atlantic lowland forests of northeastern Costa Rica. It is classified as Tropical Wet Forest in the Holdridge system (Hartshorn and Peralta 1988). La Selva is warmer and wetter than the Kauai sites at the oldest extreme of the Hawaiian substrate age gradient. In addition to being wetter, La Selva also receives more nitrate, calcium, and potassium in rainfall than does Kauai (2.5, 5.7, and 3.2 kg·ha<sup>-1</sup>·yr<sup>-1</sup> vs. 0.2, 1.4, and 0.5 kg·ha<sup>-1</sup>·yr<sup>-1</sup> for La

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TABLE 1. Comparison of properties between our study sites on Kauai (Hawaii, USA) and at La Selva (Costa Rica).

Characteristic	Kauai	La Selva
Bedrock type	basalt	basaltic andesite
Bedrock age (millions of years)	4.1	1.2 <sup>†</sup>
Mean annual temperature (°C)	16	26
Mean annual rainfall (m/yr)	2–5	4
Dominant tree species and family	<i>Metrosideros polymorpha</i> (Myrtaceae)	<i>Pentaclethra macroleoba</i> (Mimosaceae)
Stems (%)	>75 <sup>‡</sup>	12
Litterfall (g·m <sup>-2</sup> ·yr <sup>-1</sup> )	424 <sup>‡</sup>	726–836 <sup>§</sup>
Native N fixers	no	yes
Transect elevation change (m)	<100	<30

Notes: Kauai data are from Vitousek (2004), and La Selva data are from Parker (1994), Sollins et al. (1994), and Clark and Clark (2000). “Stems (%)” is the percentage of stems within the plot area that are *M. polymorpha* or *P. macroleoba*.

<sup>†</sup> This is the youngest bedrock date from La Selva (Alvarado 1990).

<sup>‡</sup> At rainfall of 2.5 m/yr.

<sup>§</sup> Six-year mean litterfall (leaves and twigs <1 cm diameter; D. A. Clark, unpublished data).

Selva and Kauai, respectively) (Eklund et al. 1997, Carrillo et al. 2002). However, both areas support deep (>5 m) Oxisols derived from volcanic parent materials of similar ages: the Kauai site sits atop 4–5 Ma basalt (Ma is mega annum, or 10<sup>6</sup> years old; Crews et al. [1995]), and La Selva’s soils are derived from basaltic andesites thought to be ~1.2 Ma (Alvarado 1990). However, the latter date was determined by potassium argon dating, which is subject to high errors in weathered rock; thus La Selva’s bedrock age is less well constrained than that of the Kauai lavas. Geomorphically stable soils at both sites are believed to be depleted in rock-derived nutrients, with low levels of exchangeable cations and phosphorus (MacDonald et al. 1983, Vitousek and Denslow 1987, Sanford et al. 1994, Sollins et al. 1994, Crews et al. 1995, Kitayama et al. 1997, Veldkamp et al. 2003, Vitousek 2004). Each is also dominated by a single tree species (on Kauai, *Metrosideros polymorpha*; at La Selva, the nitrogen fixer *Pentaclethra macroleoba*), which allowed us to compare foliar nutrient concentrations for a single species at different landscape positions. Despite these similarities, the old-growth forests at La Selva are much more diverse and have double the annual fine litterfall (and presumably greater NPP) than forests on Kauai (Vitousek 2004; D. A. Clark, unpublished data). The two areas are compared geologically and biologically in Table 1.

We sampled soils and foliage in six 0.5-ha plots established for an ongoing landscape-scale study of carbon cycling at La Selva (the Carbono Project) and additional sites along La Selva’s south boundary (Fig. 1). All of our sampling occurred on the oldest residual soils at La Selva: the Matabuey, Jaguar, and Esquina series (from oldest to youngest; Sollins et al. 1994, Clark et al. 1998). The Matabuey and Jaguar ridge top soils were originally classified as Typic Tropohumults by Sollins et al. (1994), but the Matabuey recently has been reclassified as a Typic Haploperox (M. Kleber, personal communication). The younger Esquina soils are thought to derive from the same flow as the Matabuey, but have been classified as Andic Humitropepts

because they lack argillic horizons (Sollins et al. 1994). Because we did not do detailed soil analyses on the Esquina soils, we only report results from the Esquina soils when they differ from the patterns observed on the older residual soils.

#### Sample collection and analyses

We collected upper canopy full-sun leaves (using a shotgun) and soils in October 2003, and additional samples in April 2005. In each sloped Carbono plot (“steep Ultisol” plots, after Clark and Clark [2000]), we ran a transect from a ridge top, through the plot, to the valley bottom. No transect was longer than 100 m nor descended more than 30 m in elevation. The slopes in these plots ranged from 13° to 25°, as measured from a 1-m digital elevation model (DEM) of La Selva. Slopes are steeper, up to 30°, along the south boundary. Each Carbono plot contains grid posts placed every 10 m, and the south boundary trail is marked every 50 m, so it was possible to measure position very accurately along the slope for each sample taken. We calculated relative elevation (RE) using the 1-m DEM; RE is defined as the elevation change between the highest point on a toposequence (ridge top) and a given point. Thus ridge tops have RE = 0, and the bottom of our longest slope had RE = –29 m.

We used a shotgun to collect canopy leaves of *P. macroleoba* and other canopy trees, as well as palm fronds; only full-sun leaves and fronds were selected. Each reported value represents the analysis of a composite sample consisting of several leaves from a single tree. Plant samples were ground and analyzed for C and N using a Carlo Erba NA1500 series II elemental analyzer (Carlo Erba, now Thermo Electron, Milan, Italy). A second subsample of leaf material was ashed at 505°C, dissolved in nitric acid, and analyzed for P and cations (Ca, Mg, K) using induction coupled plasma mass spectrometry (ICP-MS; inductively coupled plasma mass spectrometry). A third subsample was used for Sr isotope analyses.

Soils (free of surface litter) were collected at 5-m spacing along transects from ridge top to valley bottom

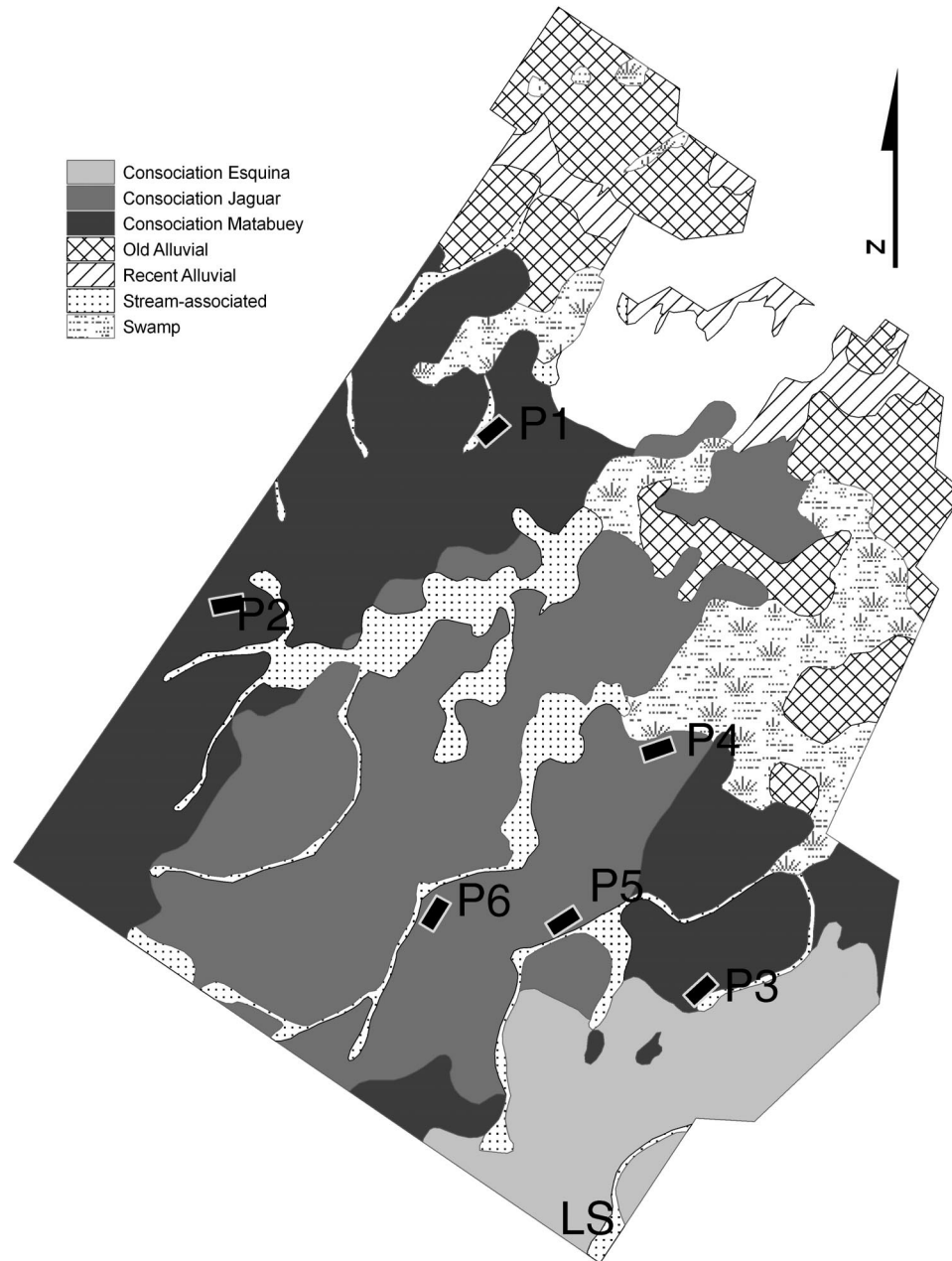


FIG. 1. Modified soil map of La Selva Biological Station, Costa Rica. The areas that we examined are marked by white boxes and are labeled P1–6 (Carbono Plots) and LS. Residual soils are Esquina, Jaguar, and Matabuey. The figure is modified from a digital soils map of La Selva (*available online*: (<http://www.ots.ac.cr/en/laselva/gis.shtml>)).

(11 samples per plot), using a bulb corer to a depth of 15 cm in the mineral soil. Soils were stored in coolers, shipped to Stanford University, and analyzed for Bray's extractable phosphorus within 10 days of collection. The detection limit of our autoanalyzer (Alpkem RFA/2, Alpkem, Wilsonville, Oregon, USA) was 0.08  $\mu\text{g/g}$  (Bray and Kurtz 1945). Additional soil samples at four depths (0–10, 10–30, 30–50, and 50–100 cm) had been collected earlier at six locations along contour lines at the top, middle, and bottom of the Carbono slope plots;

these were aggregated by depth and contour, dissolved in concentrated nitric acid at 170–190°C and 1000–1700 kPa for 8 hours, and were analyzed for total P by ICP-AES, inductively coupled plasma-atomic emission spectrometry (König and Fortmann 1996). Recovery rates using this method were >95% (E. Veldkamp, *personal communication*).

In April 2005, we collected additional plant and soil samples from ridge tops on the residual soils for analysis of Sr isotopes and immobile element concentra-

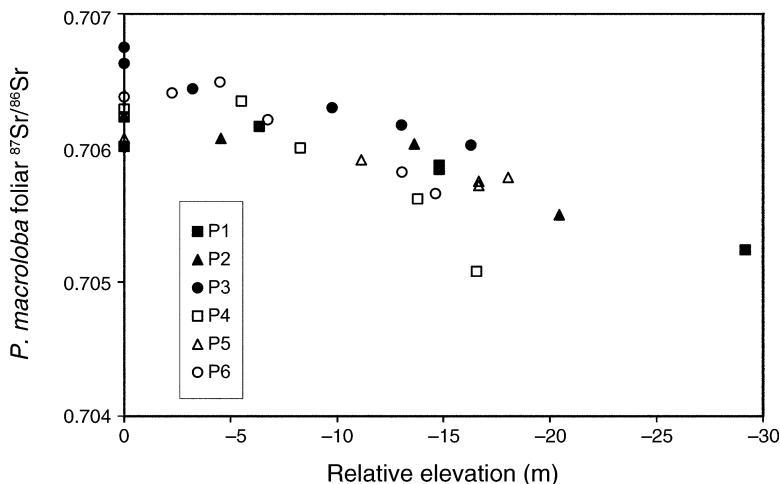


FIG. 2. Change in foliar  $^{87}\text{Sr}/^{86}\text{Sr}$  along slopes for the dominant tree *Pentaclethra macroloba*. In each plot, *P. macroloba* leaves were sampled from trees located along a transect running from the flat ridge top (relative elevation, RE = 0) to the valley bottom. RE is the change in elevation between the highest point on a transect and a given sampling point. Plots P1–3 (solid symbols) are on the Matabuey Residual soil; plots P4–6 (open symbols) are on the Jaguar Residual soil. For plots P1–6, respectively,  $r^2 = 0.79, 0.82, 0.95, 0.81, 0.93, \text{ and } 0.88$ ;  $P < 0.0001$  in all cases. Atmospheric inputs have  $^{87}\text{Sr}/^{86}\text{Sr} \approx 0.7092$  and bedrock inputs have  $^{87}\text{Sr}/^{86}\text{Sr} \approx 0.7036$ .

tions. Soil samples were taken from within the ridge top Carbono plots (“flat Ultisol” after Clark and Clark [2000]) on the Matabuey soils, and made use of 3 m deep soil pits described by Veldkamp et al. (2003). We dug two fresh pits to a depth of 1 m within 2 m of each deep pit. Soils in these new pits were sampled by depth, and the soil from the two pits was combined, for a given depth, prior to analysis. Samples at 1, 2, and 3 m depth were collected from within the deep pits. Because these pits were dug in 1997, we used a soil corer to extract samples at least 30 cm in from the pit wall to avoid edge effects. A subsample of each soil was analyzed for niobium (Nb) and zirconium (Zr) by Lithium metaborate fusion and ICP-MS by ALS Chemex Corporation (Sparks, Nevada, USA). A second subsample was extracted with 0.25 mol/L ammonium acetate; the solution was dried and analyzed for the isotopic composition of plant-available Sr.

#### Strontium systematics and analyses

Strontium isotopes have been used to trace nutrient provenance in several studies across the tropics and elsewhere (Graustein 1989, Chadwick et al. 1999, Poszwa et al. 2002, Bern et al. 2005). The approach is based on differences in the ratio of  $^{87}\text{Sr}$  to  $^{86}\text{Sr}$  in atmospheric deposition vs. rock weathering; it is often applied using a two end-member mixing model where atmospheric inputs are primarily marine aerosol ( $^{87}\text{Sr}/^{86}\text{Sr} = 0.7092$ ) and the bedrock is a geologically young mafic igneous substrate ( $^{87}\text{Sr}/^{86}\text{Sr} = 0.7036$ ; Capo et al. [1998], Kennedy et al. [1998], Whipkey et al. [2000]). These conditions are satisfied in Hawaii (Vitousek 2004); our analysis of a bedrock sample ( $^{87}\text{Sr}/^{86}\text{Sr} = 0.7037$ ), an above-canopy rainwater sample ( $^{87}\text{Sr}/^{86}\text{Sr} = 0.7089$ ), as well as La Selva’s near-coastal

location and geologic setting, indicate that the conditions are met there as well.

Strontium is most commonly used as a proxy for Ca, because the two cations have similar valence and charge. However, Sr can be a useful tracer for other rock-derived elements, including Mg, P, and K (Whipkey et al. 2000, Porder et al. 2005a), as long as differences in mobility are taken into account. For example, because P is much less mobile than Sr, the persistence of rock-derived Sr in a soil is likely to be accompanied by a greater persistence of rock-derived P (Porder et al. 2005a).

Methods for Sr isotope analysis followed those described by Porder et al. (2005a). All Sr isotopic ratios were determined using a Finnigan MAT 261 solid source mass spectrometer (Thermo Electron, Milan, Italy) at the USGS in Menlo Park or at Stanford University. Analytical blanks were usually  $< 1$  ng, and the average ( $\pm$  SE) for NBS 987 during the time of analysis was  $0.71022 \pm 0.00003$  at the USGS and  $0.71034 \pm 0.00005$  at Stanford. Samples analyzed at Stanford were normalized to the correct standard value, and sample measurements were typically precise to 0.00003 (2 SE).

## RESULTS

The ratio  $^{87}\text{Sr}/^{86}\text{Sr}$  in foliage of *Pentaclethra macroloba* ranged from 0.7068 to 0.7045, and decreased significantly ( $P < 0.001$ ) downslope along all transects (Fig. 2), demonstrating that erosion increases the fraction of plant Sr that is derived from rock weathering. Other species showed similar patterns (Table 2). Using global average values for young, mafic, igneous rock (0.7036) and for atmospheric deposition of marine aerosol (0.7092), these values correspond to a contri-



TABLE 2.  $^{87}\text{Sr}/^{86}\text{Sr}$  of plants other than *P. macroloba* from the top and bottom of each Carbono slope transect.

Plot	Species	Family	Top	Bottom
P1	<i>Inga thibaudiana</i> DC.	Mimosaceae	0.70597	0.70561
P1	<i>Welfia regia</i> W. Bull ex Mast.	Arecaceae	0.70596	0.70543
P2	<i>Protium pittieri</i> (Rose) Engl.	Burseraceae	0.70615	0.70575
P3	<i>Dystovomita paniculata</i> (Donn. Sm.) Hammel†	Clusiaceae	0.70663	0.70669
P4	<i>Dendropanax arboreus</i> (L.) Decne. & Planch.	Araliaceae	0.70632	0.70596
P5	<i>Welfia regia</i> W. Bull ex Mast.	Arecaceae	0.70646	0.70528
P5	<i>Warszewiczia coccinea</i> (Vahl) Klotzsch	Rubiaceae	0.70595	0.70542
P6	<i>Pourouma bicolor</i> Mart. subsp. <i>scobina</i> (Benoist) C. C. Berg & Heusden	Cecropiaceae	0.70629	0.70587
P6	<i>Protium pittieri</i> (Rose) Engl.	Burseraceae	0.70627	0.70596

Notes: Two sigma errors (2 SE) associated with each measurement = 0.00003. Note that every species but one has a higher  $^{87}\text{Sr}/^{86}\text{Sr}$  at the top of the slope than at the bottom, and that all have >40% rock-derived Sr.

† Not significantly different between top and bottom.

bution of rock-derived Sr of 43–84%. Analyses of a single rock and a single rainfall sample from La Selva Biological Station yielded results very similar to the average end members (0.7037 and 0.7089, respectively). The highest percentage of rock-derived Sr in *P. macroloba* foliage (84%,  $^{87}\text{Sr}/^{86}\text{Sr}$  = 0.7045) was found in valleys on the younger Esquina soils (LS, Fig. 1).

Although the pattern of decreasing  $^{87}\text{Sr}/^{86}\text{Sr}$  along slopes matches our observations in the Hawaiian Islands, the intercept ( $^{87}\text{Sr}/^{86}\text{Sr}$  on ridge tops) is quite different at La Selva. Even on ridge tops with deep Oxisols, a relatively large fraction of the Sr in tree leaves is rock derived (>43%; Fig. 2) vs. <15% on ridge tops in old substrate in Hawaii (Porder et al. 2005a).

Concentrations of most foliar macronutrients in *P. macroloba* (N, P, Ca, Mg) did not vary systematically or significantly with slope position, despite the increase in rock-derived Sr on the slopes (Fig. 3). Foliar K increased downslope on four of the six slopes, and the trend for the six slopes combined was significant ( $P < 0.01$ ).

Concentrations of available phosphorus (Bray's extractable) did not vary significantly along the slopes sampled, but total P increased downslope at all depths (5, 20, 40, and 75 cm; Fig. 4). Total P may be more indicative of bioavailable P than is Bray's extractable P, as suggested by recent work at La Selva demonstrating that total P is negatively correlated with fine-root density (J. Espeleta, *personal communication*). Exchangeable cations (K, Ca, Mg) either did not change or increased at lower relative elevations (downslope), although these trends were not consistent at different soil depths (E. Veldkamp, J. Mackensen, and D. B. Clark, *unpublished data*).

Immobile element concentrations (ash-free) in residual soils on ridge tops averaged 34 and 351 ppm for Nb and Zr, respectively (Table 3). Soil-extractable Sr from a single deep (3 m) pit on a residual soil ridge top decreased monotonically from 0.70611 in the surface horizons to 0.70499 at 3 m depth. Nearby foliage matched the signature of the upper soil horizons (0.70605; Table 4).

## DISCUSSION

The soils of La Selva and Kauai have some fundamental similarities. Both sit atop old mafic lava flows that support deep, highly weathered Oxisols. Soils in both sites have low pH (~4), Bray's P (<2  $\mu\text{g/g}$ ), and cation exchange capacity, CEC (<2 cmol positive charge/kg soil) (Olander 2004; O. Chadwick, *personal communication*; E. Veldkamp, J. Mackensen, and D. B. Clark, *unpublished data*); they are both relatively rich in organic matter. However, in Kauai, the development of a plinthite layer below the A horizon layer impedes soil water flow and affects root distributions (Lohse and Matson 2005). In La Selva, soil horizon development is weak and soil water flow is not impeded by a hardpan layer (Sollins et al. 1994). Nevertheless, the majority of fine roots occur in the upper 50 cm of soil in both sites, although some fine roots are found at least 3 m deep at La Selva (Ostertag 2001; J. Espeleta, *personal communication*; S. Porder, *personal observation*).

Above ground, however, these ecosystems differ substantially. Fine litterfall (leaves and twigs) at La Selva is twice that at Kauai (Vitousek 2004; D. A. Clark, *unpublished data*) and the canopy is three to four times taller. Foliar concentrations of N and P are significantly higher for all of our measured canopy trees on uneroded surfaces at La Selva than at Kauai ( $P < 0.001$ ; S. Porder, *unpublished data*). Above ground, La Selva is more similar to forests on young, more fertile Hawaiian soils than to those on 4.1-Ma Kauai soils.

The similarity between La Selva and younger Hawaiian sites and dissimilarity between La Selva's and Kauai extend to the effects of erosion on foliar  $^{87}\text{Sr}/^{86}\text{Sr}$  and macronutrients. In both La Selva and Kauai, slopes support relatively shallow soils (<1 m in Kauai), and plants at lower landscape positions take up more rock-derived Sr. This shift is not correlated with increases in foliar macronutrients at La Selva, whereas at Kauai, rock-derived Sr is highly correlated with foliar P (Porder et al. 2005b). However, as at La Selva, increases in rock-derived Sr on slopes in younger (0.15 Ma) Hawaiian landscapes do not correlate with in-

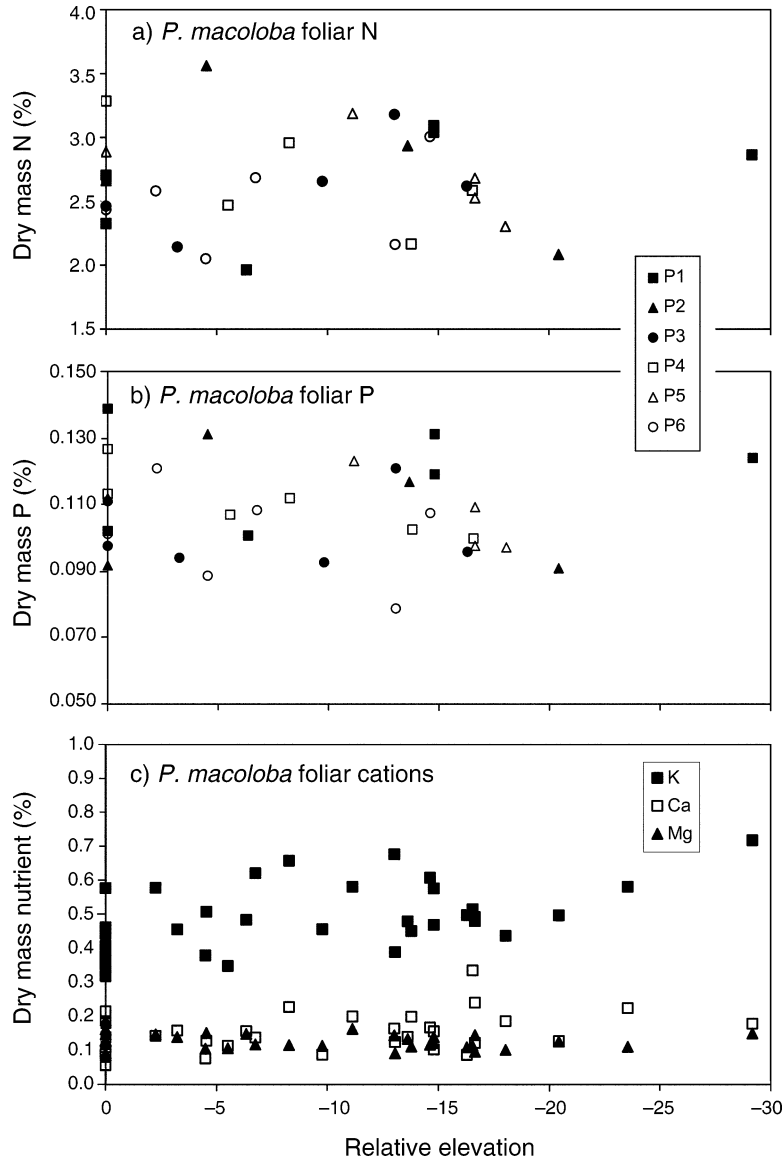


FIG. 3. *P. macoloba* foliar macronutrients (a) nitrogen, (b) phosphorus, and (c) cations show no significant trend along the slopes, except in the case of potassium. In this figure, all of the Carbono slope plots are combined.

creased foliar P, presumably because nutrients are relatively abundant in Hawaiian landscapes of this age (Porder et al. 2005a).

Why are La Selva forests more similar to those of younger, fertile Hawaiian ecosystems than to those of comparably aged Kauai? Forests on stable surfaces in Kauai take up <15% of their Sr from bedrock sources; only ~40% is derived from rock in the lowest landscape positions. In contrast, plants on stable ridge tops at La Selva take up an average of 50% of their Sr from bedrock, and up to 84% in the lowest landscape positions. Given that the soils are deep (>5 m) and the rock is highly weatherable in both places, La Selva's higher temperatures (26°C mean annual temperature) and rainfall (4 m/yr) should produce more rapid de-

pletion of rock-derived elements than at Kauai, where four million years of soil weathering produces forests almost completely dependent on atmospheric inputs of cations and P to maintain productivity in the face of leaching losses (Kennedy et al. 1998, Chadwick et al. 1999). In fact, the higher atmospheric inputs of cations at La Selva (Eklund et al. 1997, Carrillo et al. 2002) might be expected to produce an even more atmospherically dominated Sr pool at La Selva than Kauai.

We suggest three plausible explanations for the preservation of rock-derived Sr at La Selva. First, La Selva soils, even on ridge tops, may be eroding at a much faster rate than expected, with the effect of rejuvenating nutrient supply to soils at all landscape positions rather than only on slopes. Bern et al. (2005) hypothesized

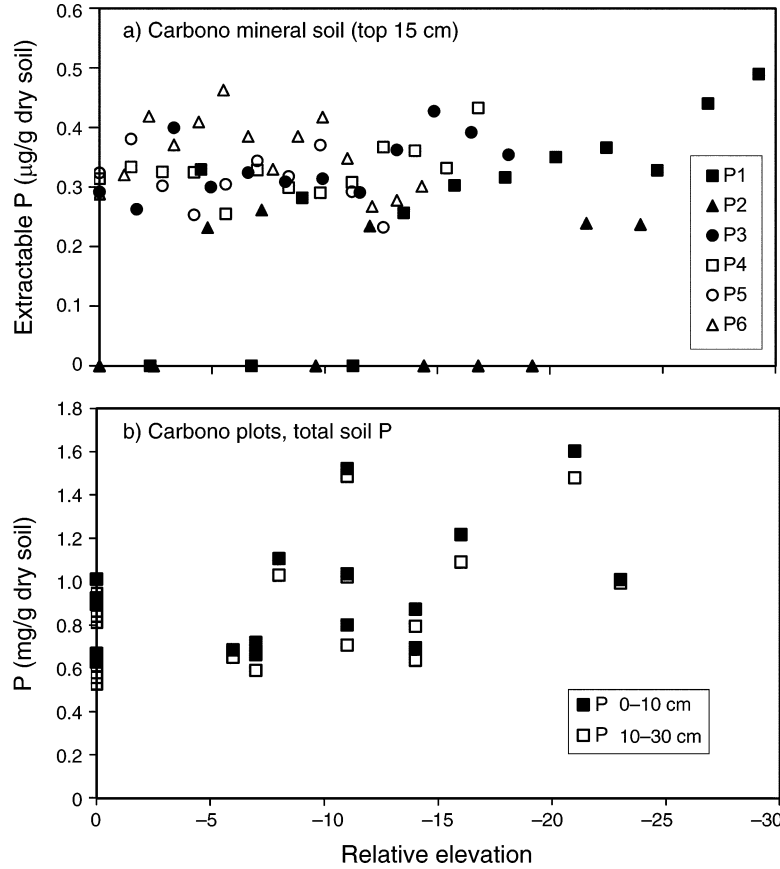


FIG. 4. (a) Upper mineral soil (top 15 cm) Bray's extractable phosphorus vs. relative elevation. Bray's increases significantly downslope ( $P < 0.01$ ) on transect P1; there is a marginally significant increase ( $P < 0.06$ ) at P3 and P4. Zero values are below the detectable limits of our method ( $0.08 \mu\text{g/g}$ ). (b) Total soil P vs. relative elevation at 0–10 and 10–30 cm depth. Trends are similar at 40 and 75 cm depth (data not shown). Six soil pits were examined along contours at the top, middle, and bottom of the slope plots. The six soil samples from a given topographic position within a plot were aggregated for analysis, and the regression for total P is significant at  $P < 0.05$  for both depths.

that the persistence of rock-derived Sr on the Osa Peninsula in western Costa Rica was related to rapid uplift and erosion rates even on ridge tops, despite the presence of apparently highly weathered Oxisols. Their model demonstrated that observed uplift rates there could provide a sufficient supply of rock-derived Sr to

explain its abundance in plants and soils. We cannot rule out this possibility based on our data, but think that uplift is unlikely to account for rock-derived Sr on La Selva ridge tops. The local topography is not nearly as steep as in Osa, La Selva sits just above the flat Atlantic lowlands, the ridge tops are relatively flat

TABLE 3. Immobile element (Nb and Zr) concentrations for three sites (L4–6) on the residual ridge tops, on an ash-free basis.

Depth (cm)	Niobium, Nb (ppm)			Zirconium, Zr (ppm)		
	L4	L5	L6	L4	L5	L6
5	37	31	33	376	318	356
20	37	31	34	422	309	365
40	35	31	34	373	314	353
75	37	33	33	366	320	346

Notes: The range for Costa Rica volcanics (lavas and tuffs) is 9.2–35.8 ppm Nb and 110–409 ppm Zr (Reagan and Gill 1989, Hannah et al. 2002). The value from each site represents a measurement of an aggregate sample from two separate pits. Detection limits are 1 and 0.5 ppm, respectively, for Nb and Zr.

TABLE 4. Ammonium acetate soil-extractable  $^{87}\text{Sr}/^{86}\text{Sr}$  from a 3 m deep soil pit on a residual ridge top, at site L5 in Costa Rica.

Soil depth (cm)	$^{87}\text{Sr}/^{86}\text{Sr}$
5	0.70611
20	0.70611
40	0.70599
75	0.70582
100	0.70572
200	0.70563
300	0.70499

Notes: Rock-derived Sr has  $^{87}\text{Sr}/^{86}\text{Sr} = 0.7036$ ; atmospherically derived Sr has  $^{87}\text{Sr}/^{86}\text{Sr} = 0.7092$ . Thus there is abundant rock-derived Sr well within the rooting zone of plants. *P. macroleba* foliage had  $^{87}\text{Sr}/^{86}\text{Sr} = 0.70605$ .

(<5°), and uplift rates, while high, are not as high as they are on the Pacific coast (Gardner et al. 1992). Furthermore, La Selva's soils do not contain clasts of unweathered basalt, which may be the proximate source of rock-derived Sr to the Osa soils (Bern et al. 2005).

Second, it is possible that nearby volcanoes in the Costa Rican Cordillera have provided inputs of ash or lahar deposits to the Atlantic lowland region. In essence, this means that the age of the bedrock (~1.2 Ma) is misleading, in that the soils are actually derived from much younger material that has been deposited more recently. The concentrations of immobile elements in soil can help to test this hypothesis, because as soils develop and mobile elements are leached, the concentration of immobile elements increases. At Kauai, for example, Nb concentrations in soil are 250–500 ppm (Vitousek 2004), whereas the basaltic parent material from which they were formed has [Nb] ~60 ppm (Kurtz et al. 2000). Along a catena on the Turrialba Volcano in Costa Rica, Zr concentrations increase from 211 ppm in unweathered volcanic ash to 597 ppm in highly weathered lowland soils (Meijer and Buurman 2003). In contrast, the La Selva residual ridge top soils have [Nb] and [Zr] 34 and 351 ppm, respectively, similar to the range reported in the literature for Costa Rican basalts and tuffs (Reagan and Gill 1989, Hannah et al. 2002). This indicates that the soils have not been heavily leached during development. This result suggests that La Selva's deep, residual Oxisols are, in fact, not as nutrient depleted as those of Kauai, and calls into question the assumption that these soils were formed from the in situ weathering of >1 Ma basaltic andesite.

The immobile element data cannot distinguish between ashfall and lahar deposits as potential agents for bringing fresh material into the system in the relatively recent past. However, the depth profile of soil-extractable Sr strongly suggests that ashfall is not the primary vector by which Sr, and other rock-derived nutrients, get into this system. Relatively continuous ashfall would produce soils with a similar Sr signature at different depths. A more recent ashfall over old soils would yield more rock-derived Sr near the surface (Kennedy et al. 1998), rather than the monotonic decrease toward the rock-derived Sr end member that we observed. Furthermore, a single large ashfall (enough to produce at least 5 m of soil) would probably cover a very large area and thus be present in ocean cores or lake deposits, but no such massive ashfall deposit has been found (Ledbetter 1985).

Finally, it is possible that plants are using deep roots to tap into nutrient-rich bedrock areas. There is little evidence of tropical trees using deep roots for nutrient acquisition, but there have been few studies of this phenomenon (see Poszwa et al. 2002). Deep rooting for nutrient uptake in arid ecosystems has been described recently by McCulley et al. (2004), and many tropical trees are thought to use deep roots for water

acquisition during the dry season (Nepstad et al. 1994, McCulley et al. 2004). Our observation of highly rock-derived Sr at 3 m depth in the soil, together with the presence of some fine roots at this depth, suggests that deep rooting (below 1 m) could contribute to the maintenance of rock-derived Sr in this forest.

We note, however, that nutrient uptake from deep in the soil may be possible only where there is a supply of nutrients within the reach of roots. If the soil weathering front has descended to depths that are inaccessible to plants, as may have occurred in the highly weathered soils of the Amazon and other deeply leached regions, deep rooting would not be able to influence the nutrient depletion of the upper soils. At La Selva, however, we suggest that deep rooting and relatively young parent material, as compared to Kauai or much of the continental tropics, combine to maintain relatively high levels of rock-derived Sr, macronutrient concentrations, and aboveground productivity.

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