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Erosion and landscape development affect plant nutrient status in the Hawaiian Islands

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Abstract We quantified variation in plant nutrient concentrations and provenance along catenas in landscapes of three different ages (0.15, 1.4, and 4.1 ma) in the Hawaiian Islands. Strontium (Sr) isotopes demonstrate that erosion provides a renewed source of rock-derived nutrients to slopes in landscapes of all ages, in some cases reversing a million years of ecosystem development in a distance of 100 m. However the effects of this input vary with landscape age. Plants on uneroded surfaces in a 0.15-ma landscape derive ~20% of their Sr from local bedrock (foliar $^{87}\text{Sr}/^{86}\text{Sr} \sim 0.7085$), while on adjacent slopes this increases to ~80% (foliar $^{87}\text{Sr}/^{86}\text{Sr} \sim 0.7045$). Despite this shift in provenance, foliar N and P do not vary systematically with slope position. Conversely, eroded slopes in a 4.1-ma landscape show smaller increases in rock-derived cations relative to stable uplands (foliar $^{87}\text{Sr}/^{86}\text{Sr} \sim 0.7075$ vs 0.7090), but have > 50% higher foliar N and P. These results demonstrate both that erosion can greatly increase nutrient availability in older landscapes, and that the ecological effects of erosion vary with landscape age. In addition, there can be as much biogeochemical variation on fine spatial scales in eroding landscapes as there is across millions of years of ecosystem development on stable surfaces.

Keywords Hawaii · Nutrient availability · Soil erosion · Strontium · Catena

Introduction

Soil scientists have long assumed that actively eroding surfaces are effectively younger than otherwise similar, stable surfaces on the same aged substrate (Jenny 1941, 1980; Gorham 1961; Walker and Syers 1976). Despite the ubiquity of eroding surfaces in most landscapes, the effects of erosion on ecosystem function have rarely been quantified. Moreover, erosion encompasses a range of processes, from gradual soil creep to frequent landslides. While the latter have been shown to remove soil and expose fresh bedrock, effectively resetting the clock for ecosystem development (Walker et al. 1996; Frizano et al. 2002), the ecological effects of less intense erosion merit further investigation.

Previous studies have demonstrated that erosion can affect biogeochemical cycles in at least two ways: (1) it can remove nutrients through physical processes (Silver et al. 1994; Scatena and Lugo 1995), and (2) it can alter the relative abundance of nutrients by exposing fresh rock to weathering, which provides a new source of rock-derived elements such as P, Ca, K and Mg, but not N (Vitousek et al. 2003). The latter effect is likely to be most important in areas where rock-derived nutrients limit important ecosystem processes. Studies that have described the relationship between topographic position (and thus levels of erosion) and nutrient availability have yielded conflicting results. For example, many have found increases in N availability downslope (Schimel et al. 1985; Hook and Burke 2000; Takyu et al. 2002) and in valley bottoms (Garten and van Miegroet 1994), though others report the opposite (Raghubanshi 1992; Silver et al. 1994), and still others report more complicated patterns (Giblin et al. 1991; Hirobe et al. 1998). At least some of these results may be caused by the hydrologic transport of mobile nutrients such as N (Giblin et al. 1991) and some may result from covariation between topography and other state factors, especially vegetation (Gartlan et al. 1986; Basnet 1992; Oliveira-Filho et al. 1994; Chen et al. 1997; Clark et al.

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1999; Condit et al. 2000). The effects of erosion on the effective age of ecosystems have received less attention than its effects on nutrient supply, in part because this analysis requires the comparison of a catena (to study the effects of erosion) to a chronosequence (to study the effects of ecosystem age in the absence of erosion).

The Hawaiian Islands provide an opportunity to isolate the effects of single state factors on ecosystem processes on both eroding and stable surfaces. The islands are formed over a mantle hot spot, which has produced a string of progressively older high volcanic islands as the Pacific plate has moved northwest over the past 5 million years (Clague and Dalrymple 1987). A chronosequence of six sites (hereafter referred to as the long substrate age gradient, or LSAG) spanning 4.1 ma of ecosystem development has been extensively studied to elucidate age-related variation in ecosystem processes (Crews et al. 1995; Vitousek et al. 1995; Vitousek and Farrington 1997; Kennedy et al. 1998; Kurtz et al. 2001; Vitousek 2004). LSAG sites are located on minimally-eroded constructional surfaces of basaltic Hawaiian shield volcanoes, receive about 2,500 mm year⁻¹ rainfall, have a mean annual temperature (MAT) ~16°C, a modern day elevation of ~1,200 m, and are dominated by the same canopy tree, ōhi'a (*Metrosideros polymorpha*). The older Hawaiian volcanoes are well dissected by streams, and exhibit ridge-slope-toeslope catenas in different-aged landscapes. Thus we were able to select catenas that had state factors (bedrock, vegetation, climate) similar to the LSAG (except for erosion).

The ōhi'a forests along the LSAG undergo a progressive transformation as initially abundant rock-derived nutrients such as P and Ca are lost from the ecosystem, and N accumulates. The youngest site (300 years) is N-limited and nutrient poor, intermediate aged sites (20 and 150 ky) are relatively nutrient rich, and the oldest site (4.1 ma) is P-limited and nutrient poor (Crews et al. 1995; Vitousek et al. 1995; Vitousek and Farrington 1997). Ōhi'a foliar nutrients track soil nutrients very closely, both in natural and fertilized settings, and we use these foliar concentrations as a proxy for nutrient availability (Vitousek et al. 1995; Vitousek and Farrington 1997).

Changes in nutrient availability and plant tissue chemistry across the LSAG correlate with a shift in cation provenance. Two geochemical tracers have been employed to analyze the percentage of rock-derived versus atmospherically-derived cation inputs to ecosystems in Hawaii and elsewhere: strontium (Sr) isotopes and Ca to Sr ratio (Ca/Sr; Graustein 1989; Kennedy et al. 1998; Kurtz et al. 2001; Blum et al. 2002). Both proxies rely on geochemical differences between atmospheric and rock sources, and use a two end-member model to calculate the percentage of rock-derived nutrients in vegetation and soil (Capo et al. 1998; Kennedy et al. 1998; Stewart et al. 1998; Whipkey et al. 2000). These tracers indicate that as Hawaiian ecosystems age in the absence of erosion, an increasing fraction of plant Sr is supplied by atmospheric deposition—80%

by 150 ky of ecosystem development and more thereafter (Kennedy et al. 1998; Chadwick et al. 1999; Kurtz et al. 2001). While the isotopic analysis only applies directly to Sr, the similarity of Sr cycling to that of Ca and Mg suggests that it can be used as a proxy for all alkaline earth elements (Graustein 1989; Capo 1998). The changes in ōhi'a foliar nutrients and Sr isotopes across the LSAG are summarized in Table 1.

The LSAG sites were deliberately placed on minimally eroded surfaces, but this chronosequence of sites is nested within a chronosequence of landscapes. The youngest sites are surrounded by other young lava flows and ash deposits, with little or no erosional topography, and relatively little biogeochemical variation. By contrast, the oldest site (Koke'e), is located on the 2% of the island of Kaua'i that has not experienced extensive erosion (MacDonald et al. 1983). Thus the stable LSAG sites represent less and less of the landscape as the Hawaiian islands age (Fig. 1).

Our study had three main goals: (1) to test the hypotheses that erosion provides a new source of rock-derived cations to slope ecosystems, (2) to test whether erosion makes ecosystems on slopes functionally equivalent to younger, uneroded, ecosystems, and (3) to test whether erosion has the same biogeochemical effects in landscapes of different ages. To this end, we compared eroding and stable surfaces within a catena in 150-ky, 1.4-ma, and 4.1-ma landscapes. All of our catenas were very close to a LSAG site, so we could determine both the effects of erosion and the magnitude of these effects relative to those resulting from ecosystem development over time.

We hypothesized that if erosion supplies a new source of rock-derived nutrients to plants on slopes, we would see increases in the percentage of rock-derived Sr in leaves. Since P is also supplied by weathering, and is less mobile than Sr, we also expected increases in soil-available P downslope. In sites where P is limiting (Koke'e LSAG site on Kaua'i) we expected this increase in soil-available P to lead to increased concentrations of foliar P. Since N is relatively abundant in older, P-limited ecosystems, we reasoned that an increase in foliar P would correlate with an increase in foliar N. However, in younger landscapes, where rock-derived elements are not limiting to plant production, we did not expect to

Table 1 Variation in ōhi'a (*Metrosideros polymorpha*) foliar N, P, Ca, ⁸⁷Sr/⁸⁶Sr, and Ca/Sr across 4.1 ma of ecosystem development. Ōhi'a is the dominant species at all long substrate age gradient (LSAG) sites. Data from Vitousek et al. (1995), Kennedy et al. (1998) and B. Weigand (personal communication)

| | Age (ky) | Wt% N | Wt% P | Wt% Ca | Ca/Sr | ⁸⁷ Sr/ ⁸⁶ Sr |
|-------------|----------|-------|--------|--------|-------|------------------------------------|
| Thurston | 0.3 | 0.87 | 0.06 | 1.58 | 263 | 0.7043 |
| Olaa | 2.1 | 1.12 | 0.097 | 1.06 | 370 | 0.7039 |
| Laupahoehoe | 20 | 1.42 | 0.0108 | 0.97 | 106 | 0.7056 |
| Kohala | 150 | 1.14 | 0.113 | 0.62 | 66 | 0.7078 |
| Kolekole | 1,400 | 1.06 | 0.085 | 0.4 | 127 | 0.7088 |
| Kokee | 4,100 | 0.86 | 0.061 | 0.42 | 85 | 0.7085 |

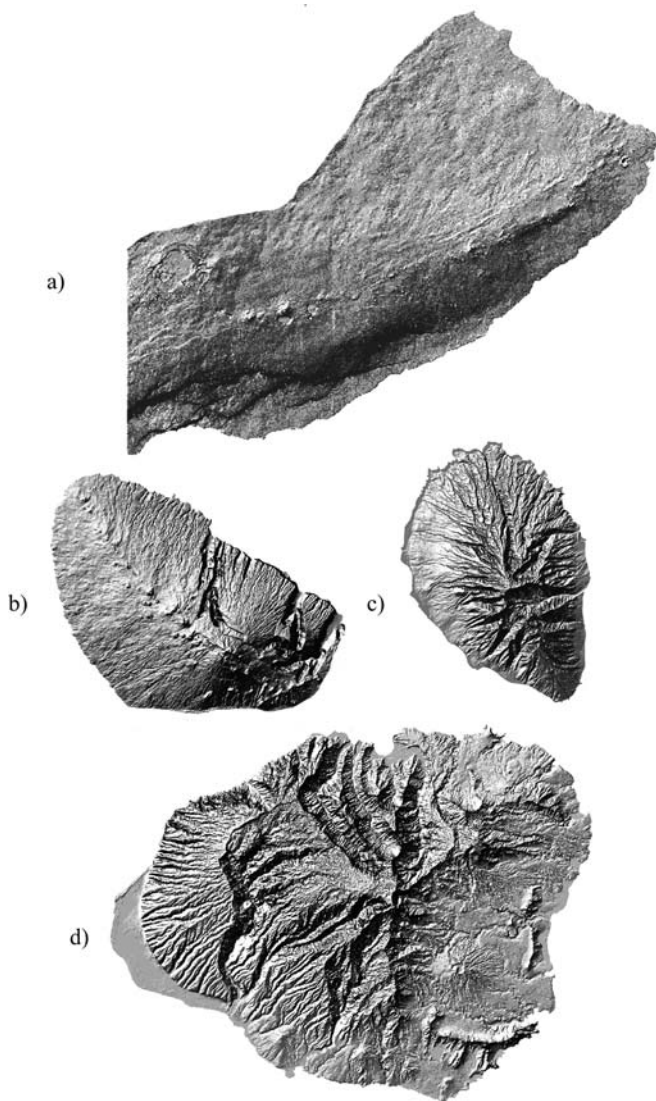


Fig. 1 The progressive erosion of landforms across the Hawaiian Islands. Digital elevation model (*DEM*) shaded relief images of **a** Kilauea, a modern volcano, **b** Kohala, an extinct, 150- to 450-ky volcano, **c** West Maui, an extinct 1.3-ma volcano, and **d** Kaua'i, an extinct 4- to 5-ma volcano. All volcanoes are shown to scale. Note the increase fluvial dissection with age. From Vitousek et al. (2003)

observe an increase in foliar nutrients associated with increases in rock-derived Sr in leaves.

Materials and methods

Site locations

We sampled and compared plants and soil from catenas in landscapes of three different ages: Kohala mountain (150 ky), Molokai (1.4 ma), and Kaua'i (4.1 ma), and compared leaf and soil nutrient concentrations and provenance. All of the catenas are situated on basaltic bedrock, are dominated by *ōhi'a*, receive rainfall of 2,500–3,500 mm year⁻¹, and consist of a stable volcanic

shield surface and a slope that drops away from that shield. Some also contain a small (a few square meters) flat depositional area, and all end at a stream. There is no floodplain development at any site. Catenas with landslide scars were excluded, except for one catena in Kaua'i where we estimate the landslide age to be many thousands of years (Vitousek et al. 2003). We did not directly measure rainfall or cloud water deposition along our catenas, but because the catenas are relatively short (the longest is 150 m) we make the assumption that atmospheric deposition rates are the same within a given catena. There is no difference in seasonality across the sites. We measured ecosystem variables as a function of relative elevation, the magnitude of elevation change between a given point on a catena and the geomorphically stable shield surface above it.

Kohala

Our sites on Kohala Mountain are underlain by the oldest exposed alkalic basalt on the island (Wolfe and Morris 1996). The Kohala LSAG site (150 ky) is one of the two most fertile sites along the chronosequence, with high levels of *ōhi'a* foliar N + P (see Table 1) and soil-available nutrients (Crews et al. 1995). We sampled two catenas, one adjacent to the Kohala LSAG site at 1,122 m (Parker Ranch) and one (Big Valley) on similar aged bedrock but at higher elevation (1,300 m) and rainfall (~3,500 mm year⁻¹; Giambelluca et al. 1986). The shield soil at the top of the catena is a Hydric Hydrand at Parker Ranch (Vitousek 2004); extensive soil classification was not done on the Big Valley shield soil, but the slope soils at both sites are Inceptisols. Both valleys are V-shaped. The slope at Parker Ranch is relatively shallow (~25°) and short (total relative elevation ~20 m). We were able to sample two parallel transects down this slope; both yielded similar results and the data have been combined in our analyses. Neither transect at Parker Ranch included a depositional area. Big Valley is larger (total relative elevation ~100 m) and steeper (~40°). In addition to the shield and slope, there is a small (tens of square meters) depositional area at the base of the slope. The soil of the depositional area is deep (> 1 m), with buried O horizons at depth indicating that pulsed erosion events have played a role in the development of this site.

Molokai

Our Molokai catena (Kolekole slope) is located in the Nature Conservancy Kamakou Preserve on the island of Molokai, near the Kolekole LSAG site. The soil on the shield surface is a Hydric Hydrand (Vitousek 2004), and the slope soil is an Inceptisol. The catena starts on a 1.4-ma alkalic basalt shield surface at 1,200 m, receives ~2,500 mm year⁻¹ of rain, and has a MAT of 16°C. Kolekole Slope descends into a large (~60 m total relative elevation), steep (~35°), V-shaped valley about

200 m from the Kolekole LSAG site. This catena ends in a small (3 m) cliff above a river and small depositional area, which we also sampled.

Kaua'i

Our sites are located in Na Pali-Kona Forest Reserve on the island of Kaua'i, near the Koke'e LSAG site. Koke'e is infertile, P-limited, and situated on 4.1-ma alkalic basalt. We sampled two catenas, both starting on a shield surface and running down to a stream. Both catenas receive $\sim 3,000$ mm year⁻¹ of rain, start at an elevation of 1,200 m and drop ~ 60 m down a relatively steep slope to a stream valley. One catena (Alakai Trail) is gentler ($\sim 22^\circ$) and ends in a depositional area, the other (Pu'u Nose) is steeper ($\sim 35^\circ$) and does not include a depositional area. The shield soils at Alakai Trail are classified as Humaquepts and the slope soils as Hapluands and Hydruands (Vitousek et al. 2003). The data from Alakai Trail are average values taken from Vitousek et al. (2003). A terrace area on the lower slope, thought to be an ancient landslide deposit, has been omitted from this analysis. Extensive soil analysis was not done at Pu'u Nose, and soil measurements are not reported from that catena.

Analyses

We collected the youngest fully mature sun leaves of *ōhi'a*, and leaves from a number of other understory species, for Sr isotope, N, P and cation analysis. Sun leaves were collected with a slingshot or a shotgun. On selected transects, soil samples were collected for analysis of available P. Soils were sampled on the catenas that were closest to the LSAG sites. All statistical analysis was performed using SYSTAT 8.0 (SPSS, Chicago, Ill., USA). All reported correlations and regressions have $P < 0.05$ unless otherwise noted in the text.

Isotopic analysis

For Sr isotopic analysis, leaf samples were ground in a plastic mixer mill and then ashed for 4 h at 505°C in a muffle furnace. They were then dissolved in distilled concentrated HNO₃ and diluted with water before ion-chromatography and analysis by induction-coupled plasma mass spectrometry (ICP-MS). Sr aliquots were obtained using standard ion-chromatography and Bio-rad AG-50×8 cation exchange resin. Sr ratios were measured on a Finnigan MAT 262 thermal ionization mass spectrometer (TIMS) at Stanford University or a Finnigan MAT 261 at the United States Geological Survey (USGS) Menlo Park. Data was normalized to $^{86}\text{Sr}/^{88}\text{Sr} = 0.1194$. The average for NBS-987 during the time when our samples were run was 0.71027 ± 0.00003 (2σ) at Stanford and 0.71024 ± 0.00002 (2σ) at USGS, and there was no instrument effect on the results.

Plant nutrient analysis

N analysis was performed on a Carlo Erba NA 1500 nitrogen/carbon/sulfur analyzer. NIST apple leaves and acetanilide were used as accuracy controls, and ran within $\pm 5\%$ of the accepted values. P and cation analyses were performed on an ICP-MS (Perkin Elmer Elan 6000) at the USGS in Menlo Park. Plant samples were ashed at 505° for at least 4 h, dissolved in distilled concentrated nitric acid and then diluted with distilled water before analysis. NIST 1515 apple leaves were processed along with our samples to check for elemental loss. Recoveries on all reported elements from standard materials were $> 95\%$.

Soil nutrient analysis

Kohala and Molokai soils were collected with a bulb corer to a depth of 15 cm in the mineral horizon after separate sampling of the O horizon and kept refrigerated until analysis, which took place within 2 weeks of sampling. Because many of the slope soils in Kohala did not have an organic layer, only the mineral soil data are shown here. However, the O-horizon, where present, showed similar trends to the upper mineral soil. Soils were hand picked to remove roots and rocks. Following a procedure modified from Kuo (1996), approximately 5 g field moist soil was placed in a flask with 125 ml water and a resin bag containing 1 g anion exchange resin (Bio-rad AG 1-X8) and 1 g cation exchange resin (DOWEX HCR-S; Kuo 1996). The flask was shaken for 24 h, and the resin bag was extracted with 0.5 N HCl. The extract was analyzed for P on an Alpkem autoanalyzer at Stanford University. Recoveries for solutions of known concentration were $100 \pm 2\%$. Soil-available P for the Kaua'i catena (from Vitousek et al. 2003) was determined by in situ incubation of anion exchange resin bags placed 10 cm below the surface for 30 days (Binkley and Matson 1983). This difference in methodology prevents direct comparison of soil-available P between Kaua'i and the other sites, but is sufficient to demonstrate a trend within a site. For bulk soil (and rock) analysis, samples were ashed at 550°C for 4 h, dissolved in a mixture of distilled HF and HNO₃, dried, redissolved in distilled 6 N HCl, dried, and redissolved in distilled concentrated HNO₃, which was diluted with distilled water before analysis. NIST 2710 Montana Soil I was used as a procedural standard. Recovery of all reported elements was $> 95\%$.

Results

Nutrient provenance and abundance

In both Kohala catenas, the percentage of rock-derived Sr in *ōhi'a* leaves is highly dependent on relative elevation ($r^2 = 0.79$ and 0.73 at Big Valley and Parker Ranch, respectively; Fig. 2a). Moreover, scale of variation in Sr provenance is dramatic. $^{87}\text{Sr}/^{86}\text{Sr}$ values in *ōhi'a* leaves

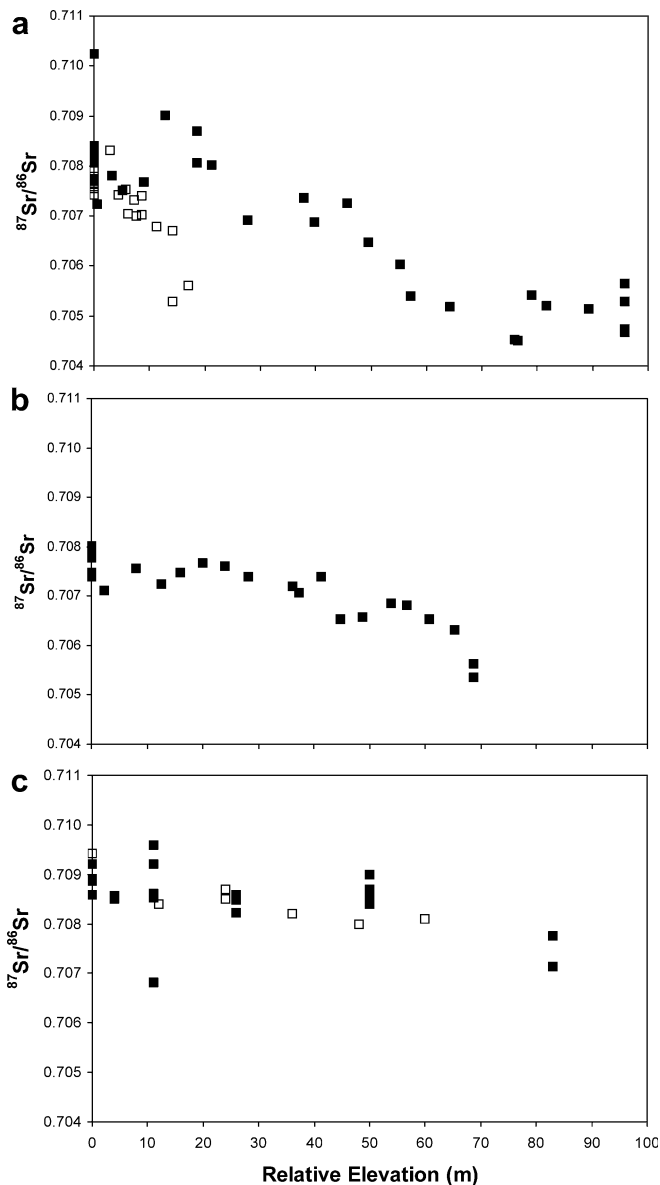


Fig. 2 Relative elevation versus $^{87}\text{Sr}/^{86}\text{Sr}$ in the youngest fully mature ōhi'a (*Metrosideros polymorpha*) sun leaves for Kohala (a) Molokai (b) and Kaua'i (c). Ōhi'a is the dominant canopy tree at all catenas. Relative elevation is defined as the magnitude of elevation change between a given point and the highest point on the catena. Seawater $^{87}\text{Sr}/^{86}\text{Sr}$ is ~ 0.7092 and Hawaiian basalt $^{87}\text{Sr}/^{86}\text{Sr}$ is ~ 0.7035 . Open symbols are Parker Ranch in Kohala ($r^2 = 0.73$, $P = 7e^{-8}$) and Pu'u Nose in Kauai ($r^2 = 0.73$, $P = 0.001$). Filled symbols are Big Valley in Kohala ($r^2 = 0.79$, $P = 5e^{-12}$), Kolekole slope in Molokai ($r^2 = 0.71$, $P = 3e^{-6}$) and Alakai Trail in Kauai ($r^2 = 0.17$, $P = 0.02$)

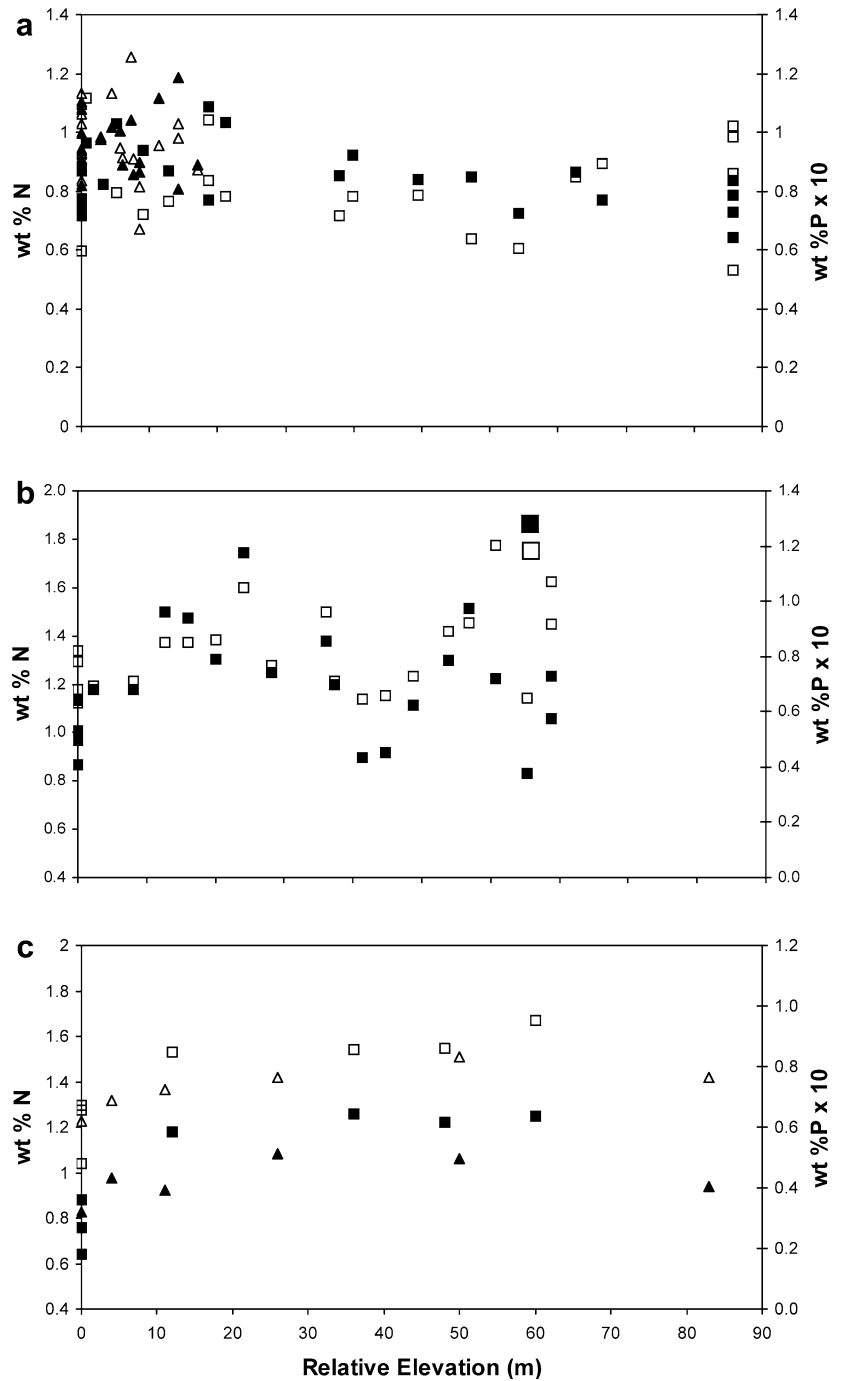
along the transect in Big Valley (total relative elevation ~ 100 m and a distance of ~ 150 m) vary from an average of 0.7081 on the shield surface to 0.7045 on the lower slope, a transition from $\sim 20\%$ to $> 80\%$ rock-derived Sr. *Dicranopteris linearis* (Gleicheniaceae), a common understory climbing fern, has a $^{87}\text{Sr}/^{86}\text{Sr}$ of 0.7078 on the shield at Big Valley and 0.7049 on the lower slope. At Parker Ranch, similar variation (0.708–0.705) in ōhi'a foliar $^{87}\text{Sr}/^{86}\text{Sr}$ occurs over an elevation

change of ~ 17 m and a distance of 42 m. This variation is equivalent to that seen across 150 ky of ecosystem development on uneroded surfaces along the LSAG, as the $^{87}\text{Sr}/^{86}\text{Sr}$ value of ōhi'a leaves on the lower slopes is similar to that of ōhi'a leaves at the 300-year LSAG site (Kennedy et al. 1998). Despite this shift in the availability of rock-derived cations, plant N and P levels do not change consistently downslope (Fig. 3a), although soil-available P increases (Fig. 4a). Although we have only a few tree fern (*Cibotium* spp.) samples from this transect, they show no trend in foliar P either. Ōhi'a foliar Ca increases dramatically (and non-linearly) downslope at Big Valley, to levels almost as high as anywhere on the LSAG (Fig. 5).

Rock-derived Sr also increases in ōhi'a leaves on the Molokai catena (Kolekole slope, $r^2 = 0.71$; Fig. 2b), and the scale of the shift is almost as large as in Kohala. Ōhi'a leaves on the shield surface above Kolekole slope have an average $^{87}\text{Sr}/^{86}\text{Sr} = 0.7077$, corresponding to $\sim 30\%$ rock-derived Sr, while leaves on the lower slope of the catena have $^{87}\text{Sr}/^{86}\text{Sr}$ as low as 0.7063 ($\sim 50\%$ rock-derived Sr), and leaves from the depositional area have $^{87}\text{Sr}/^{86}\text{Sr}$ as low as 0.7054 ($\sim 70\%$ rock-derived Sr). Unlike the Kohala transects, increased availability of rock-derived Sr lower on Kolekole slope is associated with a slight but significant increase in leaf P ($r^2 = 0.17$, $P = 0.03$), although leaf N shows no significant trend (Fig. 3b). However, both foliar N and P levels on the slope as a whole are higher than they are on the shield and shoulder (one way ANOVA, $P = 0.02$ for P, $P < 0.06$ for N). As in Kohala, there is a large increase in soil-available P downslope (Fig. 4b).

Ōhi'a on both Kaua'i shield surfaces are very low in foliar N and P (~ 0.6 and 0.06 wt.%), and they derive most of their Sr from atmospheric sources ($^{87}\text{Sr}/^{86}\text{Sr}$ of 0.709, $\sim 5\%$ rock-derived). Rock-derived Sr increases to about $\sim 25\%$ (~ 0.7075) in leaves from the lower slopes of large catenas with total relative elevations of ~ 60 m (Pu'u Nose) and ~ 80 m (Alakai Trail; Fig. 2c). This relatively small change in Sr is associated with an $\sim 50\%$ increase in ōhi'a leaf P, and a doubling of leaf N on the lower slope (Fig. 3c). At Pu'u Nose, ōhi'a $^{87}\text{Sr}/^{86}\text{Sr}$, N and P are strongly dependent on relative elevation ($r^2 = 0.73$, 0.62 and 0.63 , respectively), while at Alakai Trail the trend is weaker ($r^2 = 0.17$, 0.08 (not significant) and 0.21 for $^{87}\text{Sr}/^{86}\text{Sr}$, N and P, respectively). However, the nutrient trend at Alakai Trail is more robust ($r^2 = 0.32$ and 0.37 for N and P, respectively) if the depositional area is excluded from the analysis. As in the other sites, soil-available P also increases downslope on Alakai Trail (Fig. 4c), although, like the other catenas, the trend is non-linear. This non-linearity may be the result of differing rates of erosion and deposition on the slope. Along the upper slope, erosion may expose new minerals to weathering, but these may be exported downslope before the nutrients they contain become available to plants. On the lower slopes, accumulation of material may allow these new minerals to weather sufficiently to produce bioavailable nutrients. This would be more important for

Fig. 3 Relative elevation versus N concentration (wt%; *solid symbols, left y-axis*) and P concentrations (wt% $\times 10$; *open symbols, right y-axis*) for *ōhi'a* (*Metrosideros polymorpha*) leaves from (a) Kohala (ns), (b) Molokai (N ns, $P r^2 = 0.17$, $P = 0.03$), and (c) Kauai (r^2 for N and P at Pu'u nose = 0.6, $P = 0.02$. r^2 for N and P at Alakai trail are 0.08, ns, and 0.2, $P = 0.01$, respectively). *Squares* represent Big Valley in Kohala (a) and Pu'u Nose in Kauai (c). *Triangles* represent Parker Ranch in Kohala (a) and Alakai Trail in Kauai (c)



P, which is relatively slow to weather out of primary minerals, than it would be for Sr, which is more easily leached.

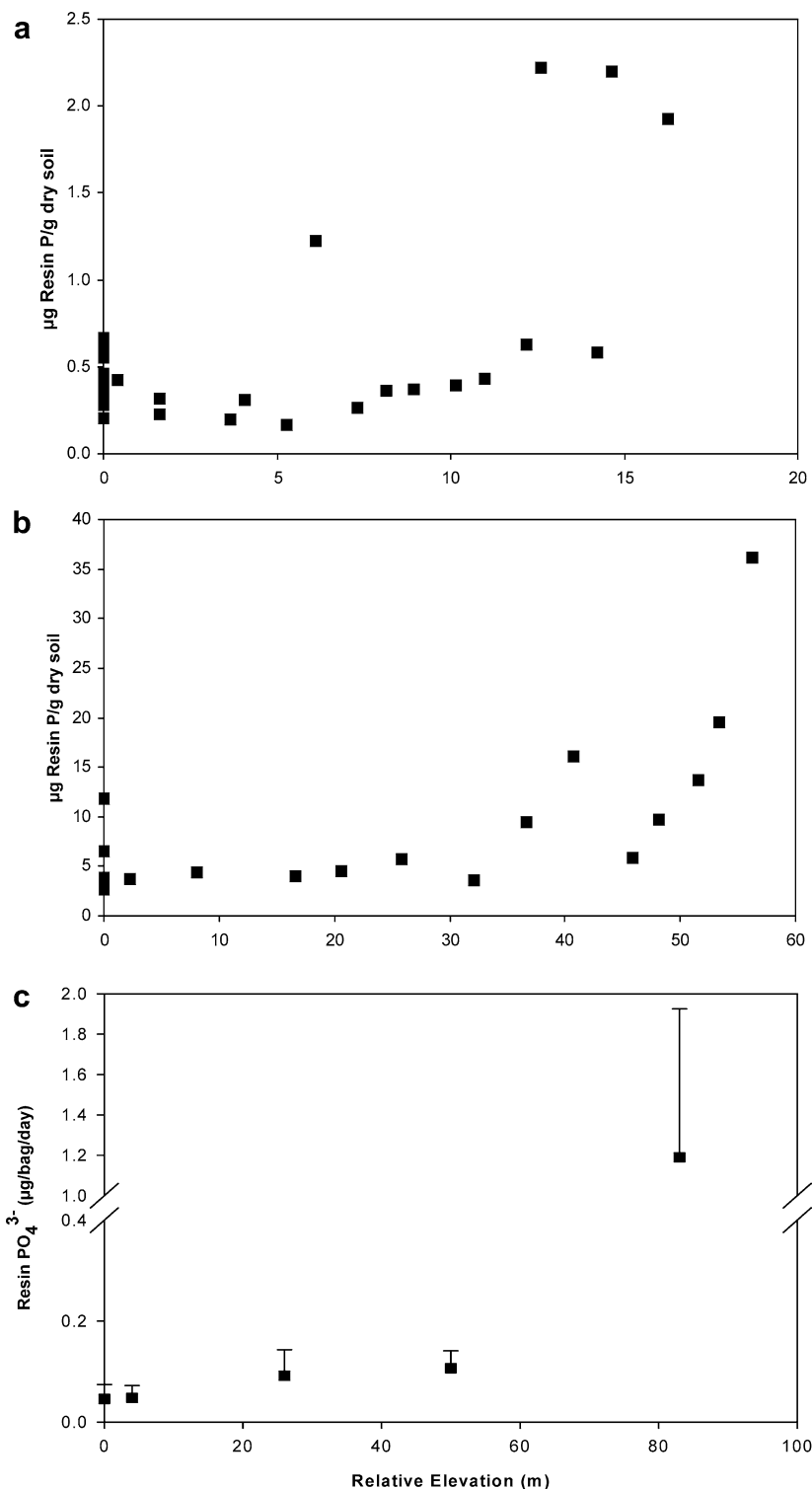
Discussion

The variable effects of erosion

These results indicate the varying effects of erosion in landscapes of different ages. In the relatively young

Kohala landscape, fresh rock is exposed to weathering on slopes, providing a large input of rock-derived nutrients and shift in foliar Sr isotopes. Concurrently, soil-available P increases significantly, but foliar nutrients show no significant changes. We believe that P and other rock-derived elements are available in sufficient supply on the shield in this relatively young landscape, and any increase in P on the slopes is not reflected in *ōhi'a* leaf P. N and P concentrations are closely correlated in *ōhi'a*, explaining the lack of trend in *ōhi'a* leaf N as well. Molokai, a landscape of intermediate age,

Fig. 4 Relative elevation versus soil available P for Kohala Parker Ranch (a) ($r^2 = 0.25$, $P = 0.04$, Molokai (b) ($r^2 = 0.36$, $P = 0.006$) and Kaua'i Alakai Trail (c) ($r^2 = 0.71$, $P = 0.07$). Because values for Kaua'i (c) are averages from Vitousek et al. (2003), we show error bars representing 1 SD. Note also that the absolute levels of soil available P are not directly comparable for the Kaua'i samples to the other two catenas because the method of analysis was different. However, Kohala and Molokai are directly comparable



exhibits an intermediate response, with moderate shifts in foliar Sr isotopes and nutrient concentrations. In this landscape even the upper slope may receive enough P via increased weathering rates to relieve ōhi'a from P-limitation. Thus increased uptake of rock-derived Sr on the lower slopes does not correspond to further increases in leaf P.

In contrast, slopes on Kauai exhibit a pronounced increase of foliar nutrients downslope while only a minor increase in rock-derived Sr. The relatively small shift in $^{87}\text{Sr}/^{86}\text{Sr}$ associated with a large trend in foliar nutrients along the Kaua'i catenas can be explained in two ways. First, even small inputs of rock-derived nutrients can have large effects if those nutrients are

limiting, as is true for P in the Kaua'i LSAG site. Second, it is possible that weathering of the bedrock by ground water, prior to exposure to near-surface soil formation, may shift the $^{87}\text{Sr}/^{86}\text{Sr}$ value of the local rock away from the value for fresh Hawaiian basalt (0.7035) and towards a higher, more seawater-like, signature. P is less mobile than Sr, so large leaching losses of rock-derived Sr would not coincide with equally large P losses. Sr concentrations in Kaua'i slope saprolites are $\sim 1\%$ of those in fresh Hawaiian basalt, while P concentrations are $\sim 25\%$ those of fresh basalts (basalt data from O.A.Chadwick, unpublished). Analysis of saprolites from slopes on Kaua'i show that the $^{87}\text{Sr}/^{86}\text{Sr}$ averages 0.7053, even though the saprolite contains vesicles and appears relatively unweathered. If water has "pre-weathered" the rock with respect to its Sr signature prior to its exposure on a slope, it is possible that relatively high inputs of rock-derived P to slope soils may not show up as similarly large changes in plant $^{87}\text{Sr}/^{86}\text{Sr}$.

Tracers of ecosystem inputs

While Sr isotopes are commonly used to indicate nutrient provenance, the ratio of Ca to Sr (Ca/Sr) has also been used to differentiate between atmospheric and rock sources (Blum et al. 2002). Along the LSAG, foliar $^{87}\text{Sr}/^{86}\text{Sr}$ in ōhi'a is negatively correlated with Ca/Sr (Pearson's $r = 0.75$; Table 1)—as would be expected if plants are increasingly dependent on atmospherically derived nutrients, because seawater (the dominant contributor to atmospheric deposition in Hawaii) has a higher $^{87}\text{Sr}/^{86}\text{Sr}$ (0.7092) and lower Ca/Sr (50) than most Hawaiian basalts. Ca/Sr is also dependent on relative elevation at all of the catenas in each age landscape in this study ($r^2 = 0.15$, $P = 0.07$ for Big Valley, $r^2 = 0.75$ for Parker Ranch, $r^2 = 0.66$ for Kolekole Slope, and $r^2 = 0.60$ for Pu'u Nose). However, Ca/Sr is *positively* correlated with the trend in $^{87}\text{Sr}/^{86}\text{Sr}$ along each catena, opposite to

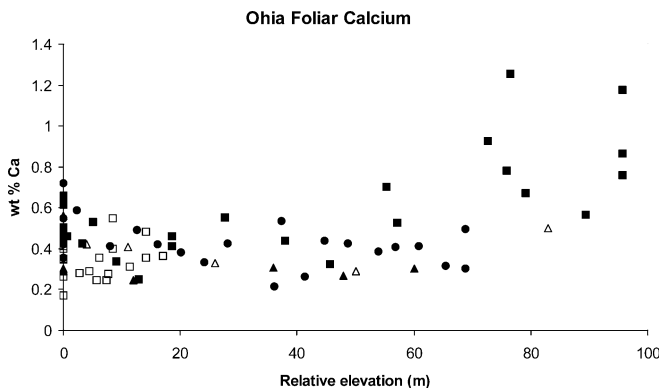


Fig. 5 Ōhi'a (*Metrosideros polymorpha*) foliar Ca (wt%) versus relative elevations for catenas in Kohala (squares), Molokai (circles) and Kaua'i (triangles). Open and closed symbols represent different catenas in the same-aged landscape. Only Big Valley in Kohala shows a significant increase in foliar Ca downslope ($r^2 = 0.43$, $P = 0.0001$)

the pattern seen across the LSAG as a whole (Fig. 6). These correlations suggest that Ca/Sr is not a consistent proxy for cation provenance in the Hawaiian system. This may be because of differences in the cycling of Ca and Sr (Poszwa et al. 2000), or variation in Ca/Sr among Hawaiian basalts (Wright and Clague 1989). Either way, the subtleties of Ca and Sr cycling must be better understood before the Ca/Sr ratio in Hawaiian plants can be considered an indicator of cation provenance.

Erosion and ecosystem age

Overall, these results suggest that the effects of erosion on functional ecosystem age depend on the age of the landscape in which the erosion is taking place, as well as the property used to quantify effective age. Using Sr provenance as a measure, rejuvenation occurs on slopes in landscapes of any age, although the rejuvenation is much more pronounced in younger systems. Using the LSAG as a scale, a functionally young slope site should have high rock-derived Sr in leaves, low foliar N + P, and low available P in soils—all properties of the young LSAG sites. Our prediction was that erosion would shift the Kohala slopes in this direction. Instead, the lower Kohala slopes exhibit relatively high levels of soil-available P, very low $^{87}\text{Sr}/^{86}\text{Sr}$, and moderate levels of foliar N and P, a combination of conditions not seen anywhere on the LSAG. The LSAG standard also suggests that functionally intermediate-aged slopes should have high foliar N and P, soil nutrient availability, and intermediate Sr isotopes. Slopes in Kaua'i fit this

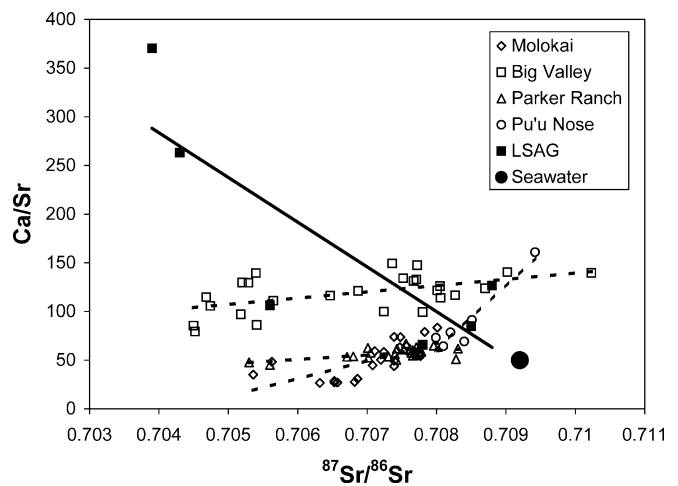


Fig. 6 Ca/Sr versus $^{87}\text{Sr}/^{86}\text{Sr}$ for ōhi'a (*Metrosideros polymorpha*) leaves from Kohala, Molokai and Kaua'i. For comparison, the long substrate age gradient (LSAG) values are also plotted, as is the value for seawater. Note that the strong positive correlation for each of the four slopes is opposite the strong negative correlation seen at the LSAG sites ($r > 0.27$, $P < 0.003$ for the Kohala catenas, $r = 0.91$, $P = 3e^{-3}$ for Molokai, $r = 0.96$, $P = 6e^{-5}$ for Kauai-Alakai Trail, and $r = 0.82$, $P = 0.04$ for the LSAG). The dashed trendlines represent the four catenas, and the solid trendline is for the LSAG

description. Although the Kaua'i slopes show the least rejuvenation using Sr as a proxy for age, they show the greatest rejuvenation using the LSAG as a standard.

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