

UNEXPECTED DOMINANCE OF PARENT-MATERIAL STRONTIUM IN A TROPICAL FOREST ON HIGHLY WEATHERED SOILS

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Abstract. Controls over nutrient supply are key to understanding the structure and functioning of terrestrial ecosystems. Conceptual models once held that in situ mineral weathering was the primary long-term control over the availability of many plant nutrients, including the base cations calcium (Ca), magnesium (Mg), and potassium (K). Recent evidence has shown that atmospheric sources of these “rock-derived” nutrients can dominate actively cycling ecosystem pools, especially in systems on highly weathered soils. Such studies have relied heavily on the use of strontium isotopes as a proxy for base-cation cycling. Here we show that vegetation and soil-exchangeable pools of strontium in a tropical rainforest on highly weathered soils are still dominated by local rock sources. This pattern exists despite substantial atmospheric inputs of Sr, Ca, K, and Mg, and despite nearly 100% depletion of these elements from the top 1 m of soil. We present a model demonstrating that modest weathering inputs, resulting from tectonically driven erosion, could maintain parent-material dominance of actively cycling Sr. The majority of tropical forests are on highly weathered soils, but our results suggest that these forests may still show considerable variation in their primary sources of essential nutrients.

Key words: atmospheric nutrients; calcium; cations; Costa Rica; isotopes; nutrient sources; parent material; strontium; tropical forest.

INTRODUCTION

New inputs of essential plant nutrients are fundamental to the structure and function of terrestrial ecosystems (Gorham et al. 1979, Schlesinger 1997). For most such nutrients, including the base cations calcium, magnesium, and potassium, ecosystem theory has long held that in situ mineral weathering dominates de novo inputs in nearly all ecosystems. However, the base cations are highly soluble in the soil solution and are easily leached from soils, especially in warmer, wetter ecosystems. These leaching losses are compensated for by continued weathering of primary minerals as long as such minerals persist in the plant-rooting zone, but in older, highly weathered soils, such as those common in tropical and subtropical regions, primary mineral pools can be largely depleted. Thus, as weathering inputs decline, the relative importance of atmospheric inputs, such as precipitation and dust, to the ecosystem's nutrient budget increases (Jordan 1982). Recent evidence has shown that atmospheric sources of these “rock-derived” nutrients can strongly influence or even dominate actively cycling ecosystem pools, especially in systems on highly weathered soils (Chad-

wick et al. 1999, Kennedy et al. 2002, Poszwa et al. 2002).

Such studies have relied heavily on the use of strontium isotopes as a proxy for base-cation cycling, the basis of which is the similarity in charge and ionic radius between Sr and Ca (Capo et al. 1998). Such Sr-isotope studies have proved highly useful in determining the relative importance of bedrock weathering vs. atmospheric sources for nutrients in certain forested ecosystems. For example, the transition from rock to atmospherically derived nutrients is striking along a soil age gradient in Hawaii. Here, Sr cycling through tropical forests growing on young, volcanic soils isotopically resembled that of the parent material, but after one million years of soil development, Sr isotopic values of foliage and soil exchangeable pools matched that of marine Sr (Kennedy et al. 1998). Likewise, a temperate Chilean forest whose soil developed from Precambrian mica schist was also shown to be dependent on marine aerosol inputs of base cations (Kennedy et al. 2002). In contrast, a tropical forest in French Guyana with a Precambrian schist and pegmatite substrate displayed leaf Sr-isotope values intermediate between the atmospheric and parent material end members, and values varied significantly depending on soil characteristics and location within the landscape (Poszwa et al. 2002). Finally, a more systematic relationship between nutrient sources and landscape position was

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TABLE 1. Characteristics of the four study sites on the Osa Peninsula, southwest Costa Rica.

Site identifier	Parent material	Soil order	Geomorphology
RMU	Osa Basalt	Ultisol	steeply (up to >40°) dissected
ABU	Osa Basalt	Ultisol	steeply dissected
RMM	Quaternary alluvium dominated by Osa Basalt	Mollisol	alluvial plain
SPU	Osa Basalt and marine sedimentary rocks	Ultisol	steeply dissected

demonstrated in Japan, where vegetation growing on soil developed from Pliocene andesite showed an increasing proportion of atmospheric Sr with increasing slope elevation (Nakano et al. 2001).

In this study we sought to determine the relative contribution of parent material vs. atmospheric sources to the nutrition of a coastal, continental tropical forest. Given the highly weathered soils and substantial sea-salt contribution to rainfall, we expected to find forests in which base-cation nutrition appeared highly dependent on marine inputs. We employed ratios of immobile trace elements to confirm the local geologic substrate as the dominant parent material for soils at our sites. Concentrations of base cations from parent material and soil were normalized to an immobile element and compared to assess depletion due to weathering and leaching. Sr served as a proxy for base-cation cycling and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios were used to determine the contribution of each end member.

METHODS

The study was conducted in lowland tropical rainforests on the Osa Peninsula of southwest Costa Rica. All sites are in primary tropical forests of high diversity, are 10 km or less from the Pacific Ocean, have a mean annual temperature of 26°C, and receive an average annual precipitation of ~5 m per year. Samples were collected from four sites representing two soil orders and three categories of parent material (Table 1). Two sites, RMU and ABU, possess Ultisols (Perez et al. 1978) and are located east of Bahia Drake on the north end of the peninsula. Both have developed on a steeply dissected landscape in the Osa basaltic complex (Berrange and Thorpe 1988, Hauff et al. 2000). Whole-rock $^{40}\text{Ar}/^{39}\text{Ar}$ dates of Osa basalts collected at RM are ~51 Ma (USGS Argon Geochronology Laboratory, [Denver, Colorado, USA], *unpublished data*). The soil at site SPU, located at San Pedrillo in Corcovado National Park, is also an Ultisol (Perez et al. 1978). However, the SPU soil developed from pelagic limestones, cherts, and argillites interstratified with the Osa basalts (Berrange and Thorpe 1988). The soil at site RMM is a less weathered Mollisol (Perez et al. 1978). It is adjacent to RMU, but developed from a complex mixture of Quaternary alluvium dominated by Osa basalt (Berrange and Thorpe 1988).

Samples of basalt parent material were collected from erosional exposures at both RMU and ABU. Soil profiles to 1 m were collected from the summit, shoul-

der, and backslope of a ridge at the RMU site. Samples were collected by 10-cm depth increments from excavated pits. Soils were oven dried and ground by agate mortar and pestle prior to analysis for bulk and trace-elements analysis by WDXRF (wavelength dispersive x-ray fluorescence) spectrometry and EDXRF (energy dispersive x-ray fluorescence) spectrometry, respectively. Precipitation samples were collected with an automated deposition sampler that opened only during rain events. Six precipitation samples, each representing a calendar month, were collected between July and December 2002. Leaf samples were collected from canopy-emergent *Brosimum utile*, a tree species common at all sites. Additional understory *B. utile* samples were collected at ABU. Samples of canopy-emergent *Schizolobium parahyba*, a legume, were collected on both RMU and RMM. The forests in all sites are exceptionally diverse, with tree species that have a broad range in foliar nutrient concentrations, but *B. utile* and *S. parahyba* represent relatively low and high ends of this range, respectively (data not shown).

Parent material and vegetation samples were digested prior to purification of strontium for isotope analysis. Vegetation samples were digested in hot, ultrapure HClO_4 (Seastar, Sidney, British Columbia, Canada) and distilled HNO_3 . Distilled HF was then added to remove residual silicate material. Rock samples were powdered and then digested in distilled HF followed by ultrapure HClO_4 (Seastar Inc.). Exchangeable strontium was leached from soils using 1 mol/L ultrapure NH_4Ac (Dionex Corporation, Sunnyvale, California, USA) Strontium was purified from all samples using Sr Spec resin (Eichrom Technologies, Darien, Illinois, USA). $^{87}\text{Sr}/^{86}\text{Sr}$ ratios were analyzed using four-collector static-mode measurements on a Finnigan MAT (Bremen, Germany) model 261 mass spectrometer at the University of Colorado. Ten measurements of SRM-987 (U.S. National Institute of Standards and Technology standard reference material) during the study period yielded a mean $^{87}\text{Sr}/^{86}\text{Sr}$ of 0.710316 ± 99 (2SD of mean). Procedural blanks for Sr extraction were 100–200 pg and could have only affected $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in the sixth decimal place. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

RESULTS

The elements Nb, Ti, and Zr are considered to be immobile during pedogenesis (Muhs et al. 1990, Kurtz

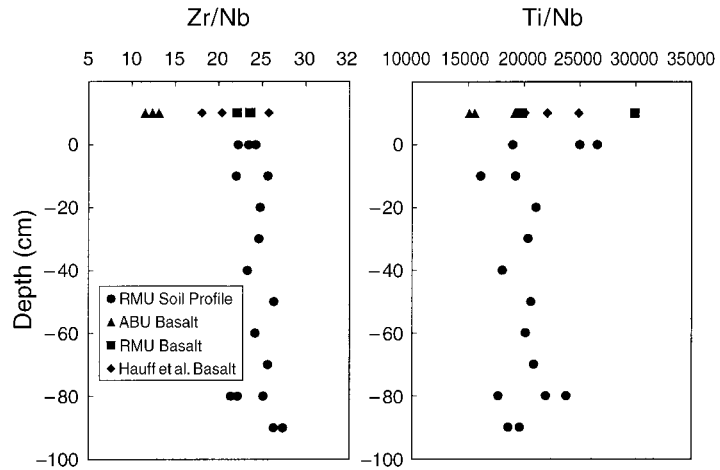


FIG. 1. Ratios of elements Zr/Nb and Ti/Nb in Osa basalt samples collected at sites RMU and ABU (Osa Peninsula, Costa Rica) and soil profiles collected at RMU. Ratios for samples collected by Hauff et al. (2000) were calculated from published concentrations; one such sample was excluded due to an anomalous Nb concentration.

et al. 2000), and calculations of Zr/Nb, and Ti/Nb ratios for soil and parent-material samples establishes the Osa basalt as the dominant parent material (Muhs et al. 1990, Brimhall et al. 1991) for the Ultisol at RMU (Fig. 1). The ratios calculated for this study are also comparable to samples of the Osa Complex collected elsewhere on the peninsula (Hauff et al. 2000), suggesting that our parent-material samples are representative of the larger complex.

The concentrations of several bulk elements were normalized to the immobile reference element Nb (Kurtz et al. 2000); comparison of these ratios between soil and parent material yields the fraction of the element remaining in the soil (Fig. 2). Despite the occasional presence of identifiable basalt fragments in some profiles, soil losses of nutrient cations Ca, Mg, K, and the tracer Sr, approach 100% except close to

the surface (Fig. 2). Such losses clearly suggest a forest growing on a highly weathered substrate. In a chronosequence study of Costa Rican soils with similar parent-material mineralogy, and under similar climatic conditions, such elemental depletion of the subsoil was observed to occur in soils 18–125 $\times 10^3$ yr in age (Nieuwenhuys and Breemen 1997).

Osa basalt and meteoric precipitation are the two end members in our Sr mixing model. The mean $^{87}\text{Sr}/^{86}\text{Sr}$ value for precipitation was 0.7088, not far removed from seawater (0.7092), as expected for a coastal ecosystem (Capo et al. 1998). $^{87}\text{Sr}/^{86}\text{Sr}$ values for parent material from RMU and ABU averaged 0.70391 and 0.70350, respectively. The distinctly different Sr isotopic values of the parent material and precipitation allow the use of isotopes to calculate the relative contribution of each potential source to the strontium cycling in the forests.

Examination of both live vegetation and the exchangeable soil pool provides an assessment of the Sr being actively cycled by the forest. The $^{87}\text{Sr}/^{86}\text{Sr}$ values of tree leaves from RMU and ABU suggest a forest still dominated by rock-derived sources of cations (Table 2). A simple, two-component isotope mixing equation using parent material and precipitation $^{87}\text{Sr}/^{86}\text{Sr}$ values as end members (e.g., Capo et al. 1998) demonstrates that for each vegetation type, rock-derived strontium accounted for $\geq 90\%$ of the foliar Sr pool. Strontium-isotope values of RMU soil leachate are very similar to those measured in the vegetation (Fig. 3), and are isotopically uniform to 1-m depth, with the exception of a slight $^{87}\text{Sr}/^{86}\text{Sr}$ increase at the surface, possibly reflecting atmospheric inputs. There is no significant variation in leachate $^{87}\text{Sr}/^{86}\text{Sr}$ with landscape position along a slope at RMU. Data from several other forests suggest that foliar $^{87}\text{Sr}/^{86}\text{Sr}$ ratios reflect those of the exchangeable pool in surface horizons (Kennedy et al. 1998, Poszwa et al. 2002); the same appears true for these Costa Rican forests. In addition, unlike some other tropical forests in drier regions (Nepstad et al.

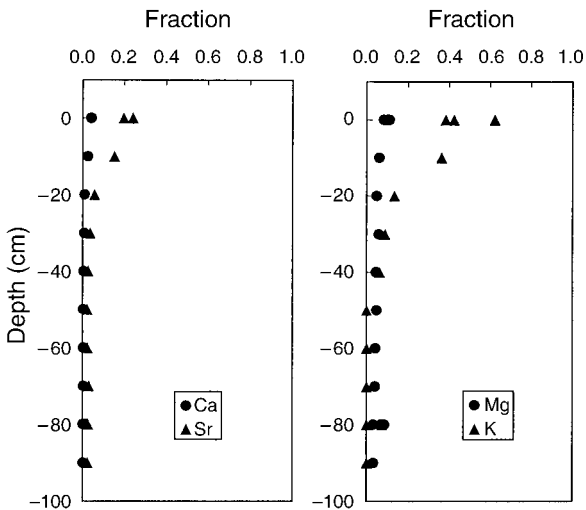


FIG. 2. Fractions of cations remaining in bulk soil at RMU. Cation concentrations in soil and RMU basalt were normalized to the immobile element Nb. The fraction of an element remaining is the Nb normalized soil value divided by the average for RMU basalt.

TABLE 2. $^{87}\text{Sr}/^{86}\text{Sr}$ ratios and Sr concentrations and molar Ca/Sr in samples from all sites.

Sample type	$^{87}\text{Sr}/^{86}\text{Sr}$	Sr (ppm)	Molar Ca/Sr	<i>n</i>
Rancho Mariposa Ultisol, RMU				
Basalt	0.7039 ± 0.0003	112 ± 45	980 ± 60	3
Rainwater	0.7088 ± 0.0004	$0.26 \pm 0.08^\ddagger$	119^\ddagger	6
<i>Brosimum utile</i>	0.7042 ± 0.0001	15 ± 7	850 ± 60	5
<i>Schizolobium parahyba</i>	0.7043 ± 0.0003	85 ± 36	490 ± 100	6
Soil leachates	0.7041 ± 0.0001	3 ± 1	200 ± 100	4
Rancho Mariposa Mollisol, RMM				
<i>B. utile</i>	0.7046 ± 0.0002	8 ± 3	1400 ± 300	6
<i>S. parahyba</i>	0.70434 ± 0.00001	21 ± 2	1300 ± 400	3
Agua Buena Ultisol, ABU				
Basalt	0.70350 ± 0.00009	120 ± 32	1300 ± 300	3
<i>B. utile</i> (canopy)	0.7034 ± 0.0002	16 ± 7	330 ± 90	5
<i>B. utile</i> (understory)	0.70401 ± 0.00004	24 ± 6	420 ± 150	5
San Pedrillo Ultisol, SPU				
<i>B. utile</i>	0.7062 ± 0.0002	16 ± 4	590 ± 40	2

Notes: Values are means \pm 1 SD, and *n* is the number of samples analyzed. Precipitation Ca/Sr is assumed to be that of seawater; its value is calculated from Capo et al. (1998). Soil leachates are from a 1-m-deep profile on the backslope of RMU.

‡ Parts per billion.

‡ This value was calculated from concentrations published in the literature, unlike other values, which were calculated from our data.

1994), our sites show little evidence of deep rooting, and therefore significant uptake of Sr from deeper soil layers seems unlikely.

There was little isotopic difference between the two tree species at RMU or between canopy and understory *Brosimum utile* at ABU. All seem to be deriving their Sr from the same ultimate (bedrock) source. $^{87}\text{Sr}/^{86}\text{Sr}$ values for *B. utile* growing on Ultisols were slightly higher at RMU compared to ABU; this difference matched a similar one in parent-material signatures. *Schizolobium parahyba* leaves from RMM and RMU were isotopically indistinguishable, but *B. utile* growing on the Mollisol had slightly higher $^{87}\text{Sr}/^{86}\text{Sr}$ values. Lower foliar concentrations of Sr in the Mollisol site are likely due to proportional uptake of Sr and Ca

(Poszwa et al. 2000) and higher Ca/Sr ratios at RMM. Leaves of *B. utile* collected at SPU had a substantially higher $^{87}\text{Sr}/^{86}\text{Sr}$ signature of 0.7062, a value intermediate between Osa basalts and the expected value in a Pliocene marine rock (~ 0.709) (Capo and DePaolo 1990). Both basalt and marine sedimentary rock contribute to the parent material for the SPU soils (Ber-range and Thorpe 1988). Thus, for all three soil types, foliar $^{87}\text{Sr}/^{86}\text{Sr}$ ratios closely match the values expected from soil parent material.

DISCUSSION

The foliar and exchangeable isotope ratios measured cannot be explained by a dust input with $^{87}\text{Sr}/^{86}\text{Sr}$ similar to that of the basalt. Long-range dust inputs from arid regions in Africa (0.714–0.717; Grousset et al. 1992) or Asia (0.705–0.721; Nakai et al. 1993) have $^{87}\text{Sr}/^{86}\text{Sr}$ values significantly higher than Osa basalt. Short-distance transport from the Mollisol at RMM to the Ultisol at RMU via dust, litter, or pollen would likewise drive RMU vegetation toward the atmospheric end member due to the generally greater $^{87}\text{Sr}/^{86}\text{Sr}$ values of the Mollisol site.

Inputs of tephra to these forests are a certainty in the geologic past. Deposits such as the Los Chocoyos ashfall blanketed large regions of Central America (Ledbetter 1985), and have $^{87}\text{Sr}/^{86}\text{Sr}$ values similar to the Osa basalts (Rose et al. 1979). However, the input of strontium to the forests on the Osa peninsula from ashfall would have been small relative to subsequent sea-salt-derived inputs. The Los Chocoyos ash has been dated to 84 000 yr BP and most large Central American ash deposits are older. A relatively strontium-rich ashfall, 1 cm thick on the Osa peninsula, could have added 608 mol Sr/ha. Using the wet-only measurements of

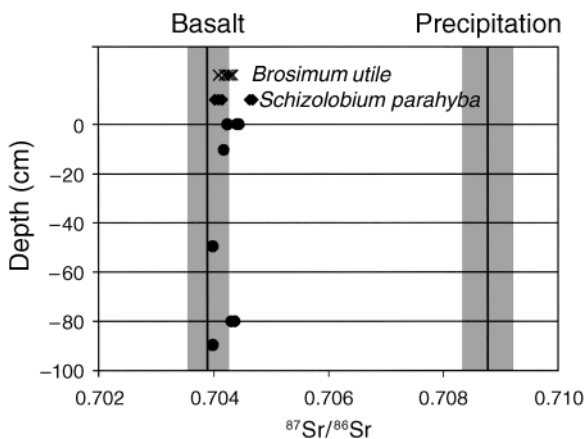


FIG. 3. $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in vegetation and in the exchange pool of three soil profiles from RMU. The vertical lines and shaded areas illustrate the mean and ± 1 SD range for RMU basalt and precipitation, respectively.

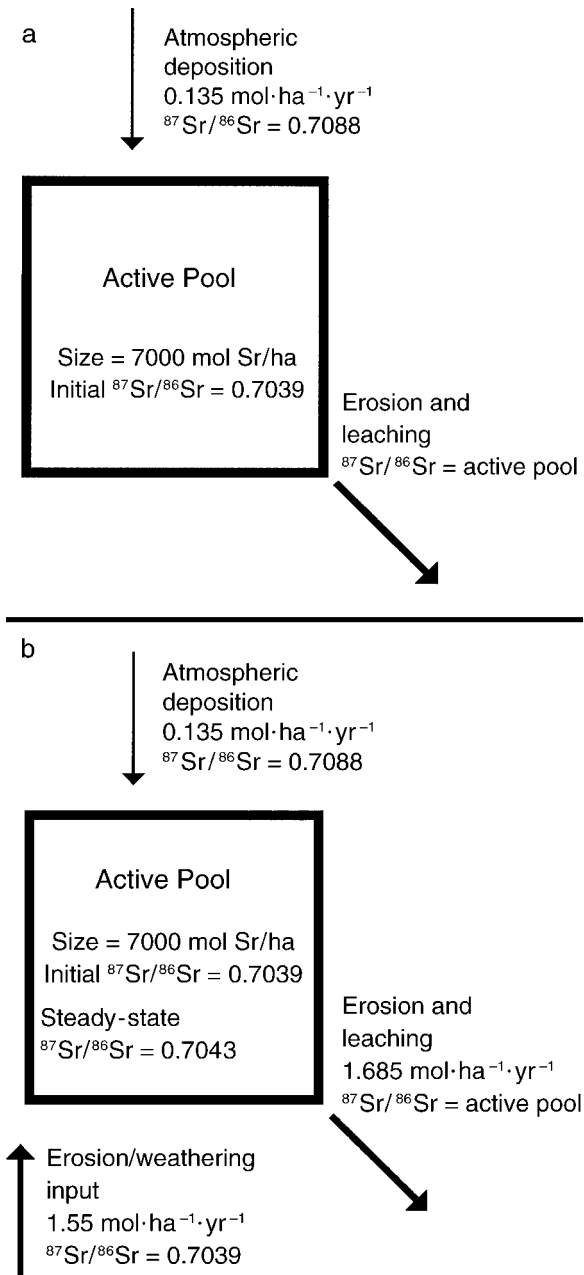


FIG. 4. Illustrations of two simple box models of Sr inputs to site RMU. (a) Atmospheric deposition is the sole chronic input. (b) Erosion-driven weathering input is added to the atmospheric deposition.

Sr inputs to our sites, we estimate that an equivalent amount of sea-salt Sr would be deposited in 4.5×10^3 yr. Thus, even large acute Sr inputs should diminish in significance relatively quickly in comparison to chronic inputs.

A simple box model (Fig. 4a) provides a useful framework for considering factors responsible for the isotopic composition of the vegetation at our Costa Rican sites. In such a model live- and dead-biomass Sr

and soil-exchangeable Sr are combined into a single active pool. Losses due to leaching and erosion are combined into a single loss term. Atmospheric deposition of sea-salt-derived Sr is the sole chronic input. Under such conditions the active Sr pool will eventually become dominated by atmospheric inputs. The relative size of inputs, losses, and the active pool serve only to control the rate of change for the isotopic composition of the active pool. An evaluation of RMU and ABU via this model would conclude that insufficient time has passed for significant amounts of atmospheric Sr to accumulate in the active pool.

An alternative model (Fig. 4b) includes an additional input of weathering-derived Sr, driven by high erosion rates. The Osa Peninsula is subject to a significant rate (2.1 to 6.5 m/1000 yr) of tectonic uplift (Gardner et al. 1992) due to the subduction of the aseismic Cocos Ridge beneath the Caribbean plate in the vicinity of the Osa Peninsula during the last 500 000 years. Significant tectonic uplift has likely maintained the geomorphic youth of the Osa in the form of steeply dissected ridges and allowed for sustained high rates of erosion even on ridgetops and high plateaus that might appear to have little chance for weathering inputs. On geologic time scales, erosion of the soil surface by soil creep, tree throw, and debris flows puts the root mat of the forest in contact with mineral matter that was previously beyond reach. Much of that mineral matter will be highly weathered saprolite, low in Sr content. However, fragments of unweathered basalt are a common feature in most sampling pits dug at RMU and ABU. Such fragments comprise only a small fraction of the soil matrix, but have Sr concentrations (~ 150 ppm) many times higher than soil (10 ppm below 30 cm) or saprolite (8 ppm). As erosion brings them in contact with the root mat, such fragments could provide a significant flux of Sr to the active pool.

Addition of a second chronic input via weathering changes the dynamic of the box model. Given sufficient time, the Sr isotopic composition of the active pool is determined purely by the relative size of the two chronic inputs. This occurs regardless of whether the active pool is aggrading, degrading, or has reached a dynamic steady state in which inputs balance losses. Thus, the active pool can achieve a steady-state isotopic composition intermediate to the two end members of the mixing model.

We evaluated sites RMU and ABU by these two models using the assumption that inputs roughly balance losses. The size of the active pool is based on current (cation-depleted soil) conditions and crudely estimated from soil and vegetation Sr concentrations to be 7000 mol Sr/ha. The active pool has an isotopic composition at time zero equal to that of basalt. The isotopic composition of basalt and the active pool is specific to each site, but atmospheric input data were available only from RMU, from which we estimate a chronic atmospheric input of $0.135 \text{ mol} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ Sr.

Without additional weathering input, the $^{87}\text{Sr}/^{86}\text{Sr}$ of the active pool exceeds any measured isotopic value after only 11 000 yr of inputs at RMU and 6000 yr at ABU. Both sites approach atmospheric dominance after 120 000 yr. With the additional weathering input, the $^{87}\text{Sr}/^{86}\text{Sr}$ of the active pool eventually achieves a steady-state intermediate of the two inputs. Assuming that the measured $^{87}\text{Sr}/^{86}\text{Sr}$ of vegetation represents a steady-state condition, that condition could be approached in 10 000 yr at either site. A weathering input to the active pool of $1.55 \text{ mol}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ Sr is required to maintain that steady state at RMU, the equivalent of weathering $900 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ of basalt. ABU would require $1.33 \text{ mol}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ Sr from $770 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ of basalt.

Such weathering rates are quite reasonable for basalt under the local climatic conditions (Dethier 1986, Wakatsuki and Rasyidin 1992). However, the rooting zone represents only a fraction of the regolith across which basalt weathering occurs, and much of the Sr released below the rooting zone is likely to be lost to leaching. Additionally, our wet-only measurement of Sr deposition likely underestimates total deposition, in which case a larger weathering input to the active pool would be required to reach steady state at measured $^{87}\text{Sr}/^{86}\text{Sr}$. Despite these caveats, this model demonstrates that a modest weathering input, driven by erosion, could prevent atmospheric inputs from dominating the local Sr cycle even in a soil that appears highly weathered. Other recent work has shown proportionally greater parent-material Sr in vegetation on a eroding hillslope in Hawaii in contrast to vegetation on a highly weathered stable surface nearby (Vitousek et al. 2003). The sustained rapid uplift and prevalence of steeper slopes at our sites may accentuate both the rate and areal extent of erosion sufficiently to maintain basalt dominance of the active Sr pool.

Sr is not a perfect proxy for Ca or other nutrient cations and thus determinations of its provenance cannot be extrapolated directly to those elements. However, examination of Ca/Sr ratios can assist in such determinations. Of the two potential sources of Ca to the system, basalt has a significantly greater Ca/Sr than sea salt (Table 2). The combination of a greater Ca/Sr and dominance of the actively cycling Sr pool suggests that basalt weathering inputs are also the dominant source of Ca. The opposing, and possibly linked, factors of preferential retention of Sr in soil and preferential Ca uptake by plants (Table 2) makes more definitive determination of proportional Ca provenance with existing data problematic.

Our results stand in stark contrast to several different recent studies that have used Sr isotopes to suggest a near-complete reliance on atmospheric inputs for nutrients largely depleted from parent-material sources (Kennedy et al. 1998, 2002). The distinct difference between our results and those for old soils in Hawaii is particularly intriguing. Both sites share basaltic parent material and significant marine inputs of base cat-

ions and Sr, yet the balance between weathering and atmospheric sources of foliar nutrients lie at opposite ends of the spectrum. The sites described here are representative of much of the Osa peninsula. Identical results from RMU and ABU, spaced 12 km apart, suggest these results are not a small-scale anomaly. Rather, we suggest that the rapid rate of tectonic uplift on the Osa peninsula is driving this regional pattern by sustaining rapid rates of erosion in all portions of the landscape. This is one aspect of our sites that differs dramatically from the Hawaiian islands, which are subsiding (Moore 1987).

The model we present here has significant implications for understanding the controls over nutrient cycling in tropical forests. It does not contradict the model presented by Chadwick et al. (1999), which outlines a transition to dominance by atmospheric inputs of nutrients as substrate becomes increasingly weathered. Rather, it suggests that under conditions that promote sustained nutrient losses, it is the competition between chronic inputs that will determine the balance of nutrient provenance. As rates of weathering, leaching, erosion, and atmospheric inputs vary among tropical forests growing on highly weathered soils, so too may their primary sources of essential nutrients.

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