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Contributions of dust to phosphorus cycling in tropical forests of the Luquillo Mountains, Puerto Rico

Julie C. Pett-Ridge

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Abstract The input of phosphorus (P) through mineral aerosol dust deposition may be an important component of nutrient dynamics in tropical forest ecosystems. A new dust deposition calculation is used to construct a broad analysis of the importance of dust-derived P to the P budget of a montane wet tropical forest in the Luquillo Mountains of Puerto Rico. The dust deposition calculation used here takes advantage of an internal geochemical signal (Sr isotope mass balance) to provide a spatially integrated longer-term average dust deposition flux. Dust inputs of P (0.23 ± 0.08 kg ha^{-1} year^{-1}) are compared with watershed-average inputs of P to the soil through the conversion of underlying saprolite into soil (between 0.07 and 0.19 kg ha^{-1} year^{-1}), and with watershed-average losses of soil P through leaching (between 0.02 and 0.14 kg ha^{-1} year^{-1}) and erosion (between 0.04 and 1.38 kg ha^{-1} year^{-1}). The similar magnitude of dust-derived P inputs to that of other fluxes indicates that dust is an important component of the soil and biomass P budget in this ecosystem. Dust-derived inputs of P alone are capable of completely replacing the total soil and biomass P pool on a timescale of between 2.8 ka and 7.0 ka, less than both the average soil residence time ($\sim$15 ka) and the average landslide recurrence interval ($\sim$10 ka).

Keywords Luquillo Mountains · Dust · Nutrient cycling · Phosphorus

J. C. Pett-Ridge (✉)
Department of Earth Sciences, University of Oxford, Oxford OX1 3PR, UK
e-mail: juliep@earth.ox.ac.uk

Introduction

Atmospheric deposition of mineral aerosol dust can provide an important input of nutrients, including phosphorus (P), to terrestrial ecosystems (Bruijnzeel 1991; Proctor 1987). Dust-derived P can contribute a major fraction of the soil P budget (Reynolds et al. 2006; Soderberg and Compton 2007), and in certain areas, dust-derived P may control ecosystem productivity (Chadwick et al. 1999; Okin et al. 2004; Swap et al. 1992). Terrestrial nutrient cycling studies tend to focus on bedrock-derived inputs of the nutrients P, K, Ca, and Mg (e.g. Vitousek and Sanford 1986), although the role of atmospheric inputs is increasingly being considered (Neff et al. 2008; Soderberg and Compton 2007; Tsukuda et al. 2006). P cycling is of particular interest in the tropics, where P may limit or co-limit ecosystem productivity (Sanchez 1976; Vitousek 1984). Tropical forests account for at least one-third of annual global terrestrial CO_2 exchange between the atmosphere and the biosphere (Field et al. 1998), and CO_2 fluxes depend on the nutrient limitations of those ecosystems. Characterizing inputs and availability of P in tropical forests remains an important task towards understanding the role of tropical forests in the global carbon cycle.

A commonly cited conceptual model of P and landscape development says that ecosystems on old, highly weathered soils (which are common in the unglaciated tropics) eventually enter a phase of P limitation (Walker and Syers 1976). The paradigm of P limitation in old tropical soils has been supported by a number of studies (Cross and Schlesinger 1995; Filippelli and Souch 1999; Sharpley et al. 1987; Tiessen et al. 1984; Vitousek and Sanford 1986; Wardle et al. 2004). Fertilization experiments have provided direct evidence of P limitation of ecological processes in tropical forests in Jamaica, Hawaii, and Costa Rica (Cleveland et al. 2006; Herbert and Fownes 1995; Tanner et al. 1990; Vitousek and Farrington 1997). P limitation of tropical ecosystems is also indirectly supported by global reviews of foliar N:P ratios showing an overall increase in N:P ratio with decreasing latitude (McGroddy et al. 2004; Reich and Oleksyn 2004), and by correlations between soil P content and both productivity and P-use efficiency (Paoli and Curran 2007; Paoli et al. 2005; Silver 1994). On the other hand, some direct tests of P limitation in the tropics have not found evidence of P limitation (Tanner et al. 1992), and clear correlations between foliar N:P and soil P content are not evident in a recent analysis of data from across Costa Rica and Brazil (Townsend et al. 2007). An alternate viewpoint is that co-limitation by both N and P is widespread in terrestrial ecosystems (Elser et al. 2007), or that a wider suite of elements including micronutrients concurrently limit production in tropical ecosystems (Kaspari et al. 2008). Other studies have highlighted the role of topography, suggesting that only lowland tropical forests are likely to be dominantly P limited, while montane tropical forests are likely to be N limited (i.e. Tanner et al. 1998). Nevertheless, the amount of direct evidence for P limitation of tropical ecosystems remains small, and simple generalizations about tropical P limitation are unlikely to be appropriate given the large variability in the tropics in soil age, soil physical properties, rainfall, uplift, erosion, and atmospheric deposition (Proctor 1987; Townsend et al. 2007; Whitmore 1989). Characterizing the P budget is also important to those tropical forests that are presently N limited, given that the predicted 120% increase in N deposition in the tropics in the next 50 years (related to trends in human activities including fossil fuel combustion) may shift the nutrient limitations of tropical systems towards P limitation (Galloway et al. 2004; Matson et al. 1999).

Globally speaking, dust is the dominant source of P in the atmosphere, although in non-dusty regions biogenic particles and combustion sources can be important (marine-derived inputs of P are negligible) (Mahowald et al. 2008). Dust-derived P may be particularly important to terrestrial ecosystems in the Caribbean, which is downwind of the Earth's largest dust source, the Sahara and Sahel regions of North Africa. Longer-term ($\geq$7 year) records show high concentrations of dust in the Caribbean atmosphere (Perry et al. 1997; Prospero and Lamb 2003). The presence African dust-derived material in Caribbean island soils has been recognized (Herwitz et al. 1996; Muhs et al. 2007; Muhs et al. 1990). However, the impact of dust inputs on terrestrial ecosystem P cycling in the Caribbean has not yet been investigated, and no direct measurements of dust deposition fluxes in the Caribbean have previously been made.

A major reason why the influence of dust on terrestrial biogeochemical cycling is understudied is that dust deposition fluxes are hard to quantify, either through direct measurement or via modeling. Dust transport is strongly affected by individual meteorological events, leading to very high spatial and temporal variability in both transport and deposition. Atmospheric deposition collectors cannot accurately measure meaningful long-term averages of total dust deposition in a forest (Hicks et al. 1980; Lindberg and Lovett 1985; Miller and Miler 1980; Stoorvogel et al. 1997; White and Turner 1970). Deposition collectors lack the surface area of the forest canopy to entrain dust and aerosols and typically do not account for spatial variability (Bruijnzeel 1989; and Bruijnzeel 1991). Relationships between leaf area index and dry deposition are strongly non-linear and appear to fall apart in montane topography (De Longe et al. 2008). Temporal variability also hampers the quantification of meaningful average dust fluxes. For example, most of the annual atmospheric input flux to a tropical ecosystem in Honduras takes place in only a few days (Kellman et al. 1982). In the Caribbean, the majority of dust transport occurs in a limited number of

Saharan dust-storm affected days (~15) out of the year, and dust transport is highly variable from year to year (Prospero et al. 1987). Calculation of net atmospheric inputs is confounded by the fact that forests themselves produce P-bearing aerosols. These biogenic internal fluxes may dominate the overall measured atmospheric P deposition. However, atmospheric P deposition is typically not apportioned into net fluxes versus internal fluxes (Artaxo et al. 1998; Graham and Duce 1981; Lesack and Melack 1996; Mahowald et al. 2005a). Likewise, indirect dry deposition estimates based on the difference between throughfall and openfall are confounded by foliar leaching, foliar uptake, and biogenic recycling (Jordan et al. 1980; Lindberg et al. 1988). Modeling atmospheric deposition is also problematic. For dry deposition, it is particularly difficult to model canopy effects because particles in the <20 μm size range are trapped more by impaction and Brownian motion under turbulent flow than by simple gravitational settling (Newman 1995). There is also considerable uncertainty in modeling wet deposition related to the choice of scavenging ratio (Mahowald et al. 2005b).

The importance of dust-derived P inputs to biogeochemical P cycling depends on the relative magnitude of inputs available through weathering of local parent material, controlled in part by tectonic setting. The rate and style of erosion is a key factor, as erosion can remove nutrients from the soil, but may also bring vegetation closer to bedrock sources. Recent work in Hawaii and Costa Rica has demonstrated that erosion increases the proportion of rock-derived nutrients measured in vegetation (Bern et al. 2005; Porder et al. 2005). In more arid environments, wind-driven erosion has the effect of depleting rather than enhancing soil nutrient pools, by preferentially removing the silt and clay-sized particles with which nutrients are primarily associated (Neff et al. 2005). In addition to tectonics and erosion, the relative importance of local bedrock versus atmospheric sources of nutrients is also a function of lithology, chemical weathering, precipitation amount, hydrological characteristics of the soil, and geographic position in relation to dust sources and transport pathways.

In this study, dust-derived P inputs are estimated based on a Sr isotope mass balance approach at the watershed scale in the Luquillo Mountains of Puerto Rico (Pett-Ridge et al. 2009). The Sr isotopic composition of long-range transported dust can be quite distinct from local sources (e.g. Biscaye et al. 1974), providing a convenient tracer to both identify and quantify dust inputs. The timescale of the dust flux estimate based on Sr isotopes is long enough (10^2–10^3 years) that it averages out the inter-annual and decadal climate fluctuations that influence short-term dust deposition fluxes. This study presents a comparison of the magnitude of the average dust-derived P flux to the magnitude of other P inputs and outputs from the combined soil and biomass P pool. On the basis of watershed-scale average fluxes, the turnover time for the total soil and biomass P pool in the Rio Icacos watershed of the Luquillo Mountains is calculated and compared to similar values calculated for the Amazon and Hawaii in order to assess the potential importance of dust-derived P inputs. The potential importance of dust-derived P inputs to overall P dynamics on varying spatial and temporal scales is also considered. Lastly, the P budget is evaluated relative to recent conceptual models relating P availability to soil age and erosion.

Site description

The Luquillo Mountains in eastern Puerto Rico include ~11,000 ha of lower montane, montane, and dwarf rainforests with elevations ranging between 250 and 1,075 m, and orographic rainfall ranging between 2,500 and 5,000 mm year^{-1} (Weaver and Murphy 1990). Within the Luquillo Mountains, the 326 ha Rio Icacos watershed (Fig. 1) ranges from 600 and 800 m elevation and is underlain by the Rio Blanco stock, an early Tertiary quartz diorite pluton (Smith et al. 1998). Other areas in the Luquillo Mountains are underlain by Lower Cretaceous volcanoclastic sediments of andesitic composition (Seiders 1974). Regolith in the Luquillo Mountains consists of highly leached ultisols, oxisols, and inceptisols, approximately 0.5–1.5 m thick, underlain by saprolite ranging in thickness from ~2 m on steep hillslopes up to 24 m on ridgetops (Simon et al. 1990). A detailed description of the vegetation, climate, and soils in the area is given by Brown et al. (1983) and in the regional soil survey (USDA NRCS 2002). Forest disturbance in the Luquillo Mountains occurs primarily through hurricanes and landslides (Scatena 1995). Landslides are triggered by heavy rains, and occur mainly as shallow soil

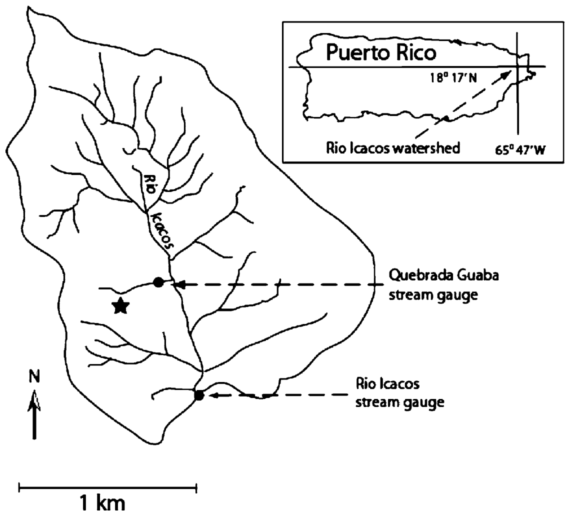

Fig. 1 Map showing the Rio Icacos watershed within the Luquillo Mountains. Star marks ridgetop site studied by Brown et al. 1995, White et al. 1998

slips and debris slides, although occasional deeper slumps also occur (Larsen and Simon 1993). The Rio Icacos watershed contains primary forest that has been largely unaffected by human impacts, with the exception of a road built through the watershed in the 1930s, but other areas of the Luquillo Mountains experienced some logging and agricultural activity in the past (Scatena and Lugo 1995).

Several studies have calculated chemical weathering fluxes and denudation velocities for the Rio Icacos watershed. Contemporary fluxes of major elements in streamwater translate into a watershed-average denudation velocity of between 58 and 75 mm ka^{-1} (Brown et al. 1995; McDowell and Asbury 1994; White et al. 1998). These estimates agree well with alternate calculations of the contemporary watershed scale denudation velocity based on Sr isotope mass balance [68 mm ka^{-1} (Pett-Ridge et al. 2009)] and mineral stoichiometry [65 mm ka^{-1} (Turner et al. 2003)]. A long-term watershed scale denudation velocity of 43 $\pm$ 15 mm ka^{-1} was calculated based on ^{10}Be in fluvial sediment (Brown et al. 1995). At the profile scale, long-term denudation velocities of 33 mm ka^{-1} [(Riebe et al. 2003), based on 60 t km^{-2} $year^{-1}$ and 2.7 g cm^{-3} density bedrock], and between 25 and 50 mm ka^{-1} (Brown et al. 1995) have been determined from ^{10}Be abundances in soils and exposed bedrock corestones. Weathering fluxes based on an analysis of saprolite porewater chemistry combined with hydrologic flux agreed well with weathering fluxes based on changes in saprolite chemistry with depth, indicating that contemporary and long-term average weathering fluxes are similar at the profile scale as well as on the watershed scale (White et al. 1998). The Rio Icacos system is considered to be approximately in steady state on the timescale of regolith development (Fletcher et al. 2006; Riebe et al. 2003; Turner et al. 2003; White et al. 1998). Denudation velocities in adjacent areas underlain by volcaniclastic bedrock are not known, but these areas have higher soil cohesive strength and exhibit less frequent landslides as compared to areas underlain by quartz diorite bedrock (Guariguata 1990; Simon et al. 1990).

The chemical and mineralogical composition of mineral aerosol dust collected throughout the Caribbean region is relatively well known (Glaccum and Prospero 1980; Herwitz et al. 1996; Holmes and Miller 2004; Perry et al. 1997; Reid et al. 2003). Most dust collected over Barbados is less than 10 µm in size, with 40–55% of the particles less than 2 µm (Prospero et al. 1970). The dust is dominated by mica/illite ($\sim$60%), and contains $\sim$10% quartz, and $\sim$5% each of kaolinite, plagioclase, calcite, and chlorite (Prospero et al. 1981).

Net atmospheric inputs of P in the Luquillo Mountains are primarily associated with desert soil-derived dust; marine-derived inputs and volcanic ash inputs are believed to be minor components, contributing less than 10% of total P deposition (Graham and Duce 1979; Graham and Duce 1981; Heartsill-Scalley et al. 2007). The Luquillo Mountains receive low levels of anthropogenic inputs due to the lack of fires in the area and because trade winds off the open Atlantic Ocean dominate the local weather.

Luquillo Mountains forest ecosystems have been described as relatively N rich (Chestnut et al. 1999), and several researchers have hypothesized P limitation, yet there is no clear consensus on nutrient limitation in the area. Fetcher et al. (1996) carried out a nutrient addition study finding that P availability appeared to limit growth of pioneer species on landslides. Silver et al. (1994) found likely evidence of P-limitation in Luquillo Mountain forests in that P-use efficiency of plants increased as soil P content declined, and that litterfall mass declined as soil P content declined.

Calculation of P mass balance for the Rio Icacos watershed in the Luquillo Mountains

This analysis of the P budget in the Rio Icacos watershed includes dust-derived atmospheric P inputs, denudation-driven inputs of P from conversion of saprolite to soil, P losses from the soil due to erosion and leaching in soil porewater, and the soil and biomass P pool sizes (Fig. 2). The lower extent of the soil pool is defined here as the soil-saprolite boundary, a conservative estimate aimed to include the deepest possible extent of plant roots. Previous work in the Rio Icacos watershed analyzing 37 soil pits found that the average soil-saprolite boundary is at 95 cm depth (Riebe et al. 2003). Roots in Luquillo Mountain forests are concentrated in the top 30 cm, with very few observed below 70 cm depth (Lawrence 1996).

The rates of saprolite production and soil and saprolite denudation are roughly equivalent on timescales of regolith development (10^4–10^5 years) based on the steady state assumption for this watershed

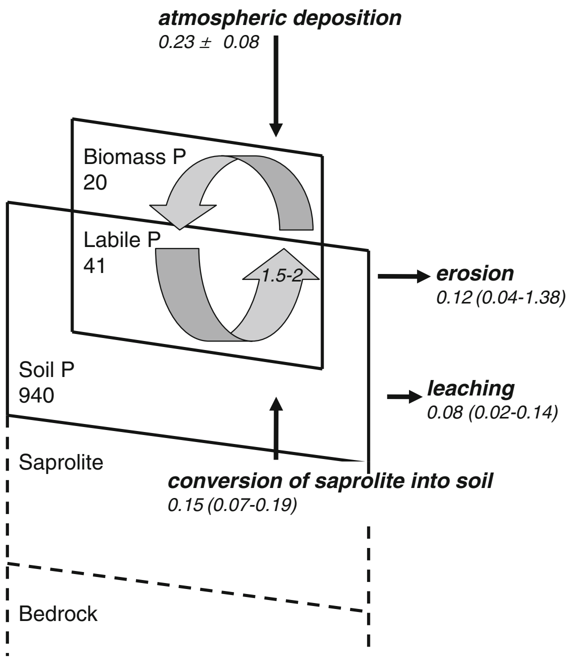

Fig. 2 Schematic of input and output fluxes to the soil and biomass P pool. Internal fluxes are shown in *grey*, net external fluxes are shown in *black*. Pool sizes are in units of kg ha^{-1} and fluxes are in kg ha^{-1} year^{-1}

(Buss et al. 2008; Fletcher et al. 2006; Turner et al. 2003; White et al. 1998). However, some evidence suggests that the modern erosion flux may be greatly accelerated (Larsen and Parks 1997). For this reason a range of estimates for each flux is presented individually, along with the relevant timescales and assumptions for each estimate.

P cycling in tropical rainforests is generally thought to be “tight”, meaning that the amount cycled within the ecosystem on an annual basis is large relative to the size of the soil pool and to the magnitude of annual inputs to the system (Jordan 1985; Newman 1995). While the internal cycling fluxes dominate P cycling on short timescales, on longer timescales, the balance between the much smaller net P input and output fluxes to and from an ecosystem becomes critical to maintaining availability of this essential plant nutrient. Because this analysis is primarily focused on longer timescales, biomass gains and losses of P (including gains and losses of biogenic atmospheric P) are assumed to roughly cancel each other out and therefore are not included in the present analysis. For the same reason, inputs of P via deposition of litter originating off-site (as opposed to internal recycling) are assumed to be equal to litter losses of P from the system. Additionally, the total P content of the soil is considered, in contrast with the common practice of focusing on labile fractions of soil P. The conversion of P from labile to unavailable or “occluded” phases (meaning insoluble or physically protected) is often considered as an output flux, but there is debate as to whether occluded forms of P are truly bio-unavailable (Johnson et al. 2003). Plants have mechanisms of accessing occluded phases over longer timescales (Janos 1980; Johnson et al. 2003; Read 1991; Richter et al. 2006; Vogt et al. 1993; Went and Stark 1968). Additionally, studies of Luquillo Mountain soils have demonstrated that intermittent anoxic conditions convert Fe(III) to Fe(II) and result in the release of soluble P from occluded phases (Chacon et al. 2006; Peretyazhko and Sposito 2005). Redox fluctuations thus appear to promote P availability in the short-term, although the effect of periodic anoxia on overall leaching losses of P over longer timescales it is not known. The choice to focus on the much larger total P pool, rather than only labile P, makes the present analysis deliberately conservative. Labile soil P pools in Luquillo ecosystems will be addressed in the discussion, however.

Dust-derived inputs of P

The average P concentration of Saharan dust in the Caribbean region is determined based on the Al content of aerosol samples (commonly measured to quantify the fraction of soil mineral aerosols within bulk aerosol samples) and P/Al ratio of Saharan dust reaching the western Atlantic basin. During especially high dust periods in Brazil, the average P/Al ratio of dust is 0.042 (Formenti et al. 2001), which is the same ratio found for Saharan dust over the Canary Islands during dust storms (Bergametti et al. 1989). Multiplying the P/Al ratio by the average 2.6 wt% Al content of Virgin Islands dust (Holmes and Miller 2004) yields 1,100 μg P g^{-1} dust as the P concentration of Saharan dust in the Caribbean. This estimate agrees well with direct measurements of P concentration in Saharan dust collected in Nigeria and Cote d'Ivoire (790 and 1,300 μg g^{-1}) (Stoorvogel et al. 1997), Mauritania (1,100 μg g^{-1} P) (Graham and Duce 1979), the eastern Mediterranean (1,100 μg g^{-1}) (Carbo et al. 2005), Europe (570–1,800 μg g^{-1} P) (Goudie and Middleton 2001), and Africa (900 ± 400 μg g^{-1}) (Ridame and Guieu 2002).

The dust flux for the Rio Icacos watershed has been calculated based on a Sr isotope mass balance (Pett-Ridge et al. 2009). To briefly summarize here, the dust flux was calculated based on Eqs. 1 and 2, which represent the streamwater Sr flux ($F^{Sr}_{streamwater}$) as the sum of contributions from measured precipitation, unmeasured dust inputs, and bedrock weathering:

$$F^{Sr}_{streamwater} = F^{Sr}_{precipitation} + F^{Sr}_{dust} + F^{Sr}_{bedrock} \tag{1}$$

$$\begin{aligned}\left(\frac{^{87}Sr}{^{86}Sr}\right)_{streamwater} F^{Sr}_{streamwater} &= \left(\frac{^{87}Sr}{^{86}Sr}\right)_{precipitation} F^{Sr}_{precipitation} \\ &+ \left(\frac{^{87}Sr}{^{86}Sr}\right)_{bedrock} F^{Sr}_{bedrock} + \left(\frac{^{87}Sr}{^{86}Sr}\right)_{dust} F^{Sr}_{dust}.\end{aligned} \tag{2}$$

The bedrock weathering flux ($F^{Sr}_{bedrock}$) and the dust flux (F^{Sr}_{dust}) were solved for and all other variables were known. The streamwater Sr flux was determined based on over 30 years of detailed discharge records and analyses of streamwater Sr concentration under a wide range of discharge conditions. The precipitation Sr flux was based on the precipitation Ca flux and the measured Ca/Sr ratio of precipitation. $^{87}Sr/^{86}Sr$ ratios of streamwater, precipitation, and bedrock were directly measured, and the $^{87}Sr/^{86}Sr$ ratio of Saharan dust was taken from previous studies of airborne dust and ocean sediment from the tropical North Atlantic (Biscaye et al. 1974; Grousset et al. 1988; Grousset et al. 1998; Grousset et al. 1992; Rognon et al. 1996). Specifically, the Sr isotope approach calculates the dust weathering flux, setting a minimum lower bound on the dust deposition flux. In Rio Icacos watershed soils, even normally weathering resistant minerals such as quartz and kaolinite are dissolving with the aid of biological activity and lower pH. The intense weathering conditions suggest that the majority of dust deposited in the soil is also weathering and contributing to streamwater fluxes, and that therefore the dust deposition and dust weathering fluxes are likely to be similar. The dust flux calculation also relies on the assumption of congruent bedrock Sr weathering, which is well-supported by available data from the Rio Icacos watershed (Pett-Ridge et al. 2009). The dust flux calculated using Eqs. 1 and 2 is 210 ± 70 kg ha^{-1} $year^{-1}$. The uncertainty is based on the standard errors of the streamwater Sr flux, the precipitation Sr flux, and each of the four $^{87}Sr/^{86}Sr$ isotope ratios in Eq. 2, and was fully propagated through the calculations. Analytical uncertainty was negligible relative to sample variance.

Multiplying the dust deposition flux for the Rio Icacos watershed (F_{dust}) of 210 ± 70 kg ha^{-1} $year^{-1}$ with the dust P concentration (C^{P}_{dust}) of 1,100 μg g^{-1} yields 0.23 ± 0.08 kg ha^{-1} $year^{-1}$ as the dust-derived P flux (F^{P}_{dust}) (Fig. 3):

$$F^{P}_{dust} = F_{dust} \times C^{P}_{dust}. \tag{3}$$

For comparison, the modeled dust-derived P deposition flux for the Northern Amazon basin ranges from 0.01 to 0.10 kg ha^{-1} $year^{-1}$ (Table 1) (Mahowald et al. 2005a). Table 1 also illustrates that those parts of western Africa receiving the strong seasonal Harmattan winds bringing Saharan dust experience some of the highest dust-derived P inputs (0.1–1.1 kg ha^{-1} $year^{-1}$, measured directly for 1 and 3 seasons) (McTainsh 1980; Stoorvogel et al. 1997; Wilke et al. 1984). For comparison, other estimates of dust-derived P inputs from the literature are also

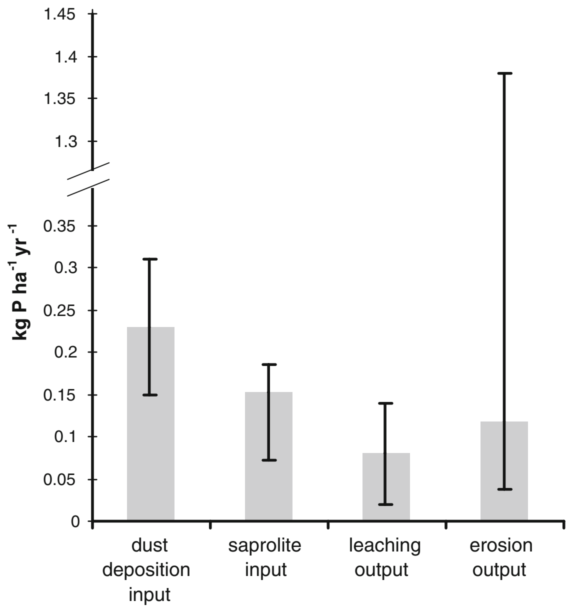

Fig. 3 Calculated net fluxes of P affecting the total soil and biomass P pools in the Rio Icacos watershed. *Error bars* for the P dust deposition flux reflect the standard error on the dust deposition calculation (Pett-Ridge et al. 2009). Note the *broken scale* on the *y*-axis. Saprolite input is based on the denudation driven conversion of saprolite to soil, calculated in Eq. 4. Upper, median, and lower estimates for saprolite input are based on denudation rates of 75 mm ka^{-1} (Brown et al. 1995), 65 mm ka^{-1} (Turner et al. 2003), and 33 mm ka^{-1} (Riebe et al. 2003), respectively. P leaching flux and uncertainty is taken from Riebe et al. (2003). The upper, median, and lower estimates of the P erosion flux, calculated based Eq. 5, employ erosion fluxes from Larsen (1997), Turner et al. (2003), and Riebe et al. (2003). The upper erosion estimate is a watershed-scale erosion flux reflecting increased landslide activity in the Rio Icacos watershed as a result of recent road construction; this estimate is heavily weighted by those areas of the landscape that have recently experienced landslides

shown in Table 1 for Hawaii (0.009 kg ha^{-1} $year^{-1}$, based on quartz accumulation, Nd isotopes, and assuming average upper continental crust [P]), Japan (0.02–0.05 kg ha^{-1} $year^{-1}$, measured directly for 3 years), and Spain (0.032 kg ha^{-1} $year^{-1}$, 11 year weekly dust sampling combined with 5 analyses of P content) (Avila et al. 1998; Kurtz et al. 2001; Tsukuda et al. 2006).

The modeled dust deposition flux for the eastern Caribbean determined by Mahowald et al. (2006) is equivalent to a P dust deposition flux of 0.06 kg ha^{-1} $year^{-1}$ using a dust P concentration of 1,100 μg g^{-1}. The grid size for this model, however, is 1.8 × 1.8°, and the dust flux is based on open ocean precipitation.

Table 1 Dust-derived P fluxes from this study as well as values reported in the literature

	Dust deposition flux of P (kg ha^{-1} $year^{-1}$)
Rio Icacos, Puerto Rico	0.15–0.31
Northern Amazon basin[a]	0.01–0.10
Central Amazon basin[b]	0.01–0.05
Hawaii[c]	0.009
Central Japan[d]	0.02–0.05
Cote d'Ivoire[e]	0.11
Nigeria[f]	1.10
Spain[g]	0.032

[a] Mahowald et al. (2005a)

[b] Swap et al. (1992) (based on water-soluble PO_4 in wet season only, December through May)

[c] Kurtz et al. (2001)

[d] Tsukuda et al. (2006)

[e] Stoorvogel et al. (1997)

[f] McTainsh (1980) and Wilke et al. (1984)

[g] Avila et al. (1998)

The P deposition flux for the Icacos watershed calculated here (0.23 ± 0.08 kg ha^{-1} $year^{-1}$) agrees well with the modeled flux for the eastern Caribbean given the ∼4-fold greater precipitation in the Luquillo Mountains as compared to the open ocean. Unfortunately, there are few ocean sediment records from the Caribbean, and therefore the model is somewhat underconstrained in this region (Kohfeld and Harrison 2001).

The estimated dust-derived P deposition value cannot be compared with direct measurements of atmospheric P deposition in the Luquillo Mountains in a meaningful way. Bulk rainfall samples are typically filtered prior to analysis and the particulate fraction is generally not analyzed. Further, measured atmospheric P deposition reflects an undetermined mixture of P derived from internal recycling of biogenic material in addition to net P inputs to the soil and biomass system (Bruijnzeel 1991; Graham and Duce 1979). The dust-derived P flux calculated here does not include internally recycled biogenic P deposition. Graham and Duce (1981) found that on the windward side of the remote island of Samoa, where rainfall is up to 5 m $year^{-1}$, 75–80% of measured atmospheric P deposition is derived from recycling of local biogenic material. Similarly, studies of both the central and northern Amazon basin have found that net inputs are only a minor fraction of total P deposition due to large internally recycled biogenic fluxes (Lesack and Melack 1996; Mahowald et al. 2005a).

Denudation-driven inputs of P to soils (conversion of saprolite to soil)

Denudation causes the soil surface to be lowered through both physical erosion and chemical weathering. At the same time the soil-saprolite and saprolite-bedrock interfaces also advance downward (Fig. 2). Relative to the soil surface, therefore, a mineral grain originating in the bedrock travels up through the regolith over time, first becoming part of the saprolite and eventually becoming part of the soil. Apatite, the primary mineral source of P, dissolves completely in the saprock zone (between bedrock and saprolite) due to extremely rapid weathering in the Rio Icacos watershed and the high susceptibility of apatite to weathering (Buss et al. 2008). As in many other tropical forests, the saprock zone throughout most of the Luquillo Mountains is far deeper than the extent of plant roots, meaning that there is essentially no primary mineral source of P to plants, with the exception of those sites having recently experienced very deep landslides (Frizano et al. 2002; White et al. 1998), or those sites where bedrock corestones are present near the surface (Fletcher et al. 2006). P present in soil and saprolite is largely hosted in fairly insoluble secondary phases, and the remainder is associated with organic matter. As a result, PO_4^{3-} concentrations are an order of magnitude lower in tributary streams draining soils in the Icacos watershed than in the main stem of the Icacos, which is dominated by solutes derived from saprock weathering (Bhatt and McDowell 2007).

The denudation driven input of P to soil ($F^{P}_{saprolite}$) is determined based on the product of saprolite P content and the denudation velocity:

$$F^{P}_{saprolite} = C^{P}_{saprolite} \times \rho_{saprolite} \times D. \tag{4}$$

The concentration of P in saprolite ($C^{P}_{saprolite}$) is 180 ± 10 μg g^{-1}, based on analyses of 32 saprolite samples from throughout the Icacos watershed (Riebe et al. 2003). The average density of saprolite ($\rho_{saprolite}$) is 1.3 g cm^{-3} (White et al. 1998). A median value for the denudation driven input of P across the saprolite-soil interface of 0.15 kg P ha^{-1} year^{-1} is determined using Eq. 4 and a modern watershed-scale denudation velocity (D) of 65 mm ka^{-1} (Turner et al. 2003) (Fig. 3). An uncertainty range of denudation-driven inputs of between 0.07 and 0.19 kg P ha^{-1} year^{-1} is determined using lower and higher estimates of the denudation velocity [33 mm ka^{-1} (Riebe et al. 2003), and 75 mm ka^{-1} (Brown et al. 1995)] and taking into account the uncertainty in saprolite P concentration. The lower estimate (0.07 kg P ha^{-1} year^{-1}) is derived from a denudation velocity based on the ^{10}Be abundances in amalgamated soil samples from 4 locations in the watershed. This estimate reflects an average over the residence time of soil (~10^4 years). The median and upper estimates (0.15 and 0.19 kg P ha^{-1} year^{-1}) are based on denudation velocities derived from contemporary streamwater fluxes.

Losses of P from soils

P losses via erosion ($F^{P}_{erosion}$) are calculated using the erosion flux (E) and the mean P concentration of soil (C^{P}_{soil}):

$$F^{P}_{erosion} = E \times C^{P}_{soil}. \tag{5}$$

A median value for the erosion flux of 1,100 kg sediment ha^{-1} year^{-1} in the Rio Icacos watershed was determined based on a contemporary watershed scale mass balance that assumes that measured dissolved streamwater fluxes are balanced by export of their residual solids, such that the sum of the dissolved and sediment fluxes equals the composition of the bedrock (Turner et al. 2003). Combining this erosion flux with the bulk P concentration of soils of 110 ± 10 μg g^{-1} [based on analyses of 91 soil samples from throughout the Icacos watershed (Riebe et al. 2003)], losses of P from the soil due to erosion are 0.12 kg P ha^{-1} year^{-1} (Eq. 5) (Fig. 3).

Other studies have determined both higher and lower erosion fluxes for the Rio Icacos watershed. Riebe et al. (2003) determined a lower erosion flux of 340 kg sediment ha^{-1} year^{-1} for the Icacos watershed using the ^{10}Be abundances in amalgamated soil samples from 4 locations in the watershed. Combining this with the soil P content (110 ± 10 μg g^{-1}) yields a P erosion flux of 0.04 kg P ha^{-1} year^{-1} (Eq. 5). The lower and median estimates of P losses via erosion are likely applicable to soils that have not recently experienced landslides, and both of these estimates employ the assumption that regolith thickness in the watershed is in steady state.

A much higher erosion flux for the Rio Icacos watershed of 9,530 kg ha^{-1} year^{-1} was determined based on contemporary measured sediment fluxes at the Rio Icacos stream gauge (Larsen 1997). This enhanced contemporary sediment flux is a far from steady state value, 70% of which is directly attributed to the building of a road through the watershed in the 1930s (Larsen 1997). To calculate an upper estimate of the P loss from erosion in this scenario, it is assumed that half of sediment export is soil and half is saprolite, such that exported sediment has a higher P concentration of 135 ± 10 μg g^{-1}. Using these values, $F^{P}_{erosion}$ is 1.38 kg P ha^{-1} year^{-1} (Eq. 5) (Fig. 3). While this upper estimate is a watershed average flux, it is not likely representative of the majority of the landscape because it is heavily weighted by the very small portion of the landscape surface area that has experienced landslides.

Losses from the soil P pool also occur through leaching, although P leaching fluxes are difficult to directly quantify in the rooting zone due to uncertainties in hydrology and very low PO_4^{3-} concentrations in soil porewater. However, soil P leaching fluxes can be calculated in a relatively straightforward manner if comparisons of soil P concentration are available over long timescales. Considering the saprolite as the precursor of the soil, depth can be used as a substitute for time. The net P loss over time can be calculated based on the decline in P content between saprolite and soil (based on comparison to an immobile index element) and the conversion of saprolite to soil (denudation velocity). In this manner Riebe et al. (2003) determined a P leaching flux in Rio Icacos soils of 0.08 ± 0.06 kg ha^{-1} year^{-1}, using Zr as the index element and basing denudation velocity on ^{10}Be abundance. This P leaching flux is shown in Fig. 3, with upper and lower estimates taken directly from the uncertainties reported by Riebe et al. (2003). Saprolite P leaching fluxes determined in the same study (0.12 ± 0.03 kg ha^{-1} year^{-1}) are relevant to biomass P cycling in landslide affected areas, where saprolite has been brought into proximity of the rooting zone. These leaching estimates rely on the assumption of regolith steady state, and reflect an average over the residence time of the soil (∼10^4 years).

Overall P budget and turnover time

The input fluxes of P to the combined total soil and biomass P pool are dust-derived inputs (0.23 ± 0.08 kg ha^{-1} year^{-1}) and saprolite-derived inputs (between 0.07 and 0.19 kg ha^{-1} year^{-1}) (Fig. 3). The output fluxes of P from the combined total soil and biomass P pool are leaching (between 0.02 and 0.14 kg ha^{-1} year^{-1}) and erosion (between 0.04 and 1.38 kg ha^{-1} year^{-1}). While there are considerable uncertainties and a range of values for each of these fluxes, Fig. 3 shows that the dust-derived flux is a non-negligible component of the soil and biomass P budget in the Rio Icacos watershed. The magnitude of the dust flux is large enough relative to the other fluxes to play an important role in maintaining long-term soil P availability. If the neighboring areas in the Luquillo Mountains underlain by volcaniclastic sediment have lower denudation rates, as is suggested by their lower landslide frequencies, thicker regolith, and lower sediment yields (Guariguata 1990; Larsen and Torres-Sanchez 1992), dust inputs may represent a larger fraction of the biogeochemical P budget there.

The importance of atmospheric P inputs to the soil and biomass system can be further evaluated by comparing P inputs to the standing pool size of P in the system. Even though some data show that the watershed is not currently in steady state, it is believed to have been in the recent past (Turner et al. 2003), and most of the watershed likely still is in steady state aside from an 85 m swath on either side of the road (Larsen and Parks 1997). Under the steady state assumption, the soil and biomass pool size divided by the total inputs gives the average turnover time (τ) for P in the total soil and biomass pool:

$$\tau^{P}_{soil+biomass} = \frac{\left(h_{soil} \times \rho_{soil} \times C^{P}_{soil}\right) + B^{P}}{\left(F^{P}_{dust} + F^{P}_{saprolite}\right)}. \tag{6}$$

The total soil P pool is 941 kg P ha^{-1}, determined by multiplying the average soil depth [h_{soil}, 0.95 m (Riebe et al. 2003)], the average soil density [ρ_{soil}, 0.9 g cm^{-3} (White et al. 1998)] and the average total P concentration of soils [C^{P}_{soil}, 110 ± 10 μg g^{-1} (Riebe et al. 2003)]. The biomass P pool (B^{P}, aboveground and forest floor) is 20 kg P ha^{-1} (Frizano et al. 2002), and the combined soil and biomass P pool is 961 kg P ha^{-1}.

Using Eq. 6, the turnover time for the combined bulk soil and biomass P pool in the Rio Icacos watershed is 2.5 ka, or between 1.8 and 4.2 ka, considering the full range of uncertainties in input fluxes and soil P concentration. For comparison, the average soil residence time in the Rio Icacos watershed is 15 ka [based on a denudation velocity of 65 mm ka^{-1}, (Turner et al. 2003)], indicating that the soil P pool turns over multiple times during the residence time of the soil. The relatively short turnover time, in combination with the fact that dust contributes approximately half the total P inputs (Fig. 3), supports the interpretation that dust-derived P is a critical part of the watershed biogeochemical P budget.

Availability of P in soil and dust

While this analysis largely focuses on the impacts of dust on long-term P budgets, dust may also be a significant component of internal biogeochemical P cycling on shorter timescales. Actively cycled, or "labile" soil P has been defined as what plants use on a timescale of less than one year, and is commonly measured using operationally-defined chemical extractions, such as the sum of resin-extractable P and HCO_3-extractable P (Johnson et al. 2003). As determined by previous work in the Rio Icacos watershed, the labile soil P pool is 41 kg ha^{-1}, and the annual P uptake is 1.5–2 kg ha^{-1} year^{-1} (based on litterfall analyses) (Frizano et al. 2002; Zarin and Johnson 1995). If all dust-associated P becomes available upon deposition into Luquillo soils, the dust flux (0.23 ± 0.08 kg P ha^{-1} year^{-1}) could supply 10–15% of the annual P uptake.

Most of the P in Saharan dust P is believed to be in the form of apatite, although exchangeable, organic, and Fe-associated forms of P are also present in Saharan dust (Eijsink et al. 2000; Herut et al. 1999; Singer et al. 2004). Phosphate ore deposits in the Western Saharan likely contribute to the apatite content (Moreno et al. 2006). Overall, limited data exists regarding the solubility of atmospheric aerosol P. Total aerosol P collected over the Atlantic Ocean, including dust, primary organic material, and biomass burning particulates, has a median solubility of 32% but a range of 0.01–87% (Baker et al. 2006b). The solubility of the Saharan dust component of total aerosols is deemed to be lower, having a median value of 8% with range of 2.3–37% (Baker et al. 2006a) or a value of roughly 15% (Herut et al. 2002). Solubility was determined by extraction in ultrapure water buffered at pH 7 with 1 mM $NaHCO_3$, a protocol that is designed to assess likely solubility in seawater (Baker et al. 2006a). Preliminary experiments on the Saharan aerosols indicated increasing solubility with decreasing pH (Baker et al. 2006b). Luquillo soils have a pH between 4 and 5 (USDA NRCS 2002), suggesting that the solubility of dust in soils may be higher. Even normally weathering-resistant minerals such as quartz and kaolinite are dissolving in Rio Icacos watershed soils (Schulz and White 1999; White et al. 1998), and therefore some apatite inclusions within dust-derived quartz may be susceptible to soil weathering. Further, dust inputs occur directly to the forest floor and root mat layer, where biological demand is highest and where microbial and mycorrhizal activity is adapted to take advantage of intermittent nutrient inputs (Lodge et al. 1994; Olander and Vitousek 2004), which may result in enhanced utilization of dust-derived P over saprolite-derived inputs. While the inputs are small and intermittent, P from dust-derived apatite is likely to be more easily made available than the occluded saprolite-derived P that is present in soil.

Temporal and spatial variability of P fluxes

The large variability of dust fluxes on daily and weekly timescales has hindered that accurate assessment of average annual inputs of atmospheric nutrients in ecosystem nutrient studies (Kellman et al. 1982). In addition, dust fluxes may vary substantially on decadal timescales. For example, atmospheric dust concentrations in Barbados increased by a factor of 4 between the 1960s and the 1980s (Prospero and Nees 1986). The relevant timescale of the P dust deposition calculation used here (Eq. 3; Fig. 3, based on Sr isotope mass balance) is assumed to provide an average over timescales of the weathering of dust-derived Sr in soil (10^2–10^3 years). Less is known about variation in dust fluxes over much longer timescales such as the residence time of the soil ($\sim 10^4$ years), which is the timescale over which soil production and denudation are argued to be in steady state in the Rio Icacos watershed. While dust loads in the global atmosphere increased considerably during the last glacial maximum, the most recent analysis (based on a coupled climate and dust source area model) suggests that dust fluxes around Puerto Rico changed by less than a factor of two (Mahowald et al. 2006).

Spatial variability in P fluxes also inevitably exists in the montane environment of the Luquillo Mountains. The ridgetop site studied by White et al. (1998) and the four hillslope sites studied by Riebe et al. (2003) all individually had denudation rates that were close to that of the watershed average (less than a factor of 1.5 difference). However, large spatial variation in soil chemistry and hydrological characteristics are observed along catenas in the Luquillo Mountains (Cox et al. 2002; Scatena and Lugo 1995; Silver et al. 1994). Ridgetop sites tend to be more stable and thus have more highly leached soils than hillslopes. Valley floor sites tend to accumulate material from upslope including organic matter and nutrients. The range in the soil production fluxes, erosion fluxes, and leaching fluxes presented in Fig. 3 are based on watershed average values and may not necessarily encompass the variability at smaller spatial scales.

The presence of near-surface bedrock corestones is an important source of spatial variability in nutrient cycling. The Rio Icacos watershed has previously been described as having "closed" nutrient cycling where mineral weathering contributions to nutrient cycling are negligible, with biomass depending instead on atmospheric inputs and tight nutrient recycling (White et al. 1998). The evidence cited for this is the lack of a gradient of primary mineral-derived nutrients such as Ca in porewater with depth in the saprolite, and the indication of complete loss of mineral nutrients at the saprolite-bedrock interface (Hamdan and Burnham 1996; White et al. 1998). However, occasional bedrock corestones of 1–4 m diameter survive the weathering environment and are visible on the surface throughout the Rio Icacos watershed (Fletcher et al. 2006). Inputs of P via apatite weathering will be much larger at those localized areas where plant roots are in contact with corestones.

Landslides, which account for 80–90% of all erosion in the Luquillo Mountains, are another important source of spatial variability (Larsen and Torres-Sanchez 1992; Larsen et al. 1999). Based on an analysis of 285 landslides triggered by Hurricane Hugo, Larsen and Torres-Sanchez (1992) determined that landslides affect 1% of the landscape in the Luquillo Mountains per hundred years, equivalent to a recurrence interval of 10 ka. Out of all landslides, 91% are characterized as shallow soil slips (0.5–1.5 m deep) and debris flows (1.5–2 m deep), while the remaining 9% are deeper slumps (Larsen and Torres-Sanchez 1992). Vegetation re-establishes on saprolite on the majority of landslide-affected sites, but bedrock is exposed during the deeper but less frequent slumps.

Dust may play a role in replenishing the labile soil P pool in the aftermath of shallow landslides. Landslide-exposed regolith has lower fertility as compared to adjacent undisturbed soils in the Luquillo Mountains (Fetcher et al. 1996; Frizano et al. 2002; Guariguata 1990; Zarin and Johnson 1995). Nearly all the phosphorus in landslide-exposed regolith in the Luquillo Mountains is biologically unavailable due to the removal of labile P, which is confined to the surface of Luquillo soils (Guariguata 1990). For example, the labile P concentrations decline from 26 $\mu g\ g^{-1}$ at 0–10 cm depth to 9 $\mu g\ g^{-1}$ at 10–35 cm depth and 3 $\mu g\ g^{-1}$ at 35–60 cm depth (Silver et al. 1999). Following landslide events, the labile P pool is gradually restored as the system recovers from the disturbance and soil organic matter content increases (Zarin and Johnson 1995). Lower fertility has also been observed in landslide-exposed regolith in Jamaica (Dalling and Tanner 1995), Ecuador (Wilcke et al. 2003), and Tanzania (Lundgren 1978).

An analysis of P budgets along a landslide recovery chronosequence in the Luquillo Mountains indicates that dust inputs may contribute roughly one-third of the biomass and labile soil P pool during landslide regeneration. P has been shown to limit plant growth on landslide-affected sites (Fetcher et al. 1996). In the aftermath of a landslide, the combined biomass and labile soil P pool recovers from dramatically depleted levels to pre-disturbance levels on a fairly short timescale of roughly 50–100 years (Frizano et al. 2002; Guariguata 1990; Myster and Fernandez 1995). Frizano et al. (2002) found that the combined biomass and labile soil P pool recovered from 6 $kg\ ha^{-1}$ on a young landslide scar to 50–70 $kg\ ha^{-1}$ in a mature ($\sim$100 year old) landslide scar. Their mass balance calculations indicated that one-third of the increase was unaccounted for (possibly deriving from occluded soil P), with the other two-thirds derived from allochthonous litter inputs and measurable precipitation inputs. Notably, the dust-derived P flux of 0.23 kg ha^{-1} $year^{-1}$ calculated here is more than enough to supply the additional one-third of P to the combined biomass and labile soil P pool. Dust-derived P inputs may therefore contribute to the remarkable resiliency of Luquillo Mountain ecosystems to disturbance (Zarin and Johnson 1995).

Comparison with P cycling in the Amazon and Hawaii

The soil P pool in the Rio Icacos watershed appears to be more sensitive to Saharan dust inputs than the soil P pool in the Amazon basin. If the soil P pool is defined over just the top 20 cm, it takes dust alone between 0.6 ka and 1.4 ka to supply the soil P content in the Rio Icacos watershed. For comparison, the Amazon basin, which is argued to be strongly dependent on P from Saharan dust for ecosystem productivity, has a timescale of 10–20 ka for the same calculation (Okin et al. 2004). The shorter timescale for the Rio Icacos watershed indicates that its soil P pool will be more responsive to changes in Saharan dust inputs as compared to the Amazon. The shorter timescale is a function of both the larger dust flux and the smaller soil P pool. The soil P pool in the Rio Icacos watershed is 198 $\pm$ 18 kg ha^{-1} in the top 20 cm (based on 941 kg ha^{-1} in the top 95 cm as discussed earlier), relative to the 354 kg ha^{-1} soil P content reported for Amazon oxisols (McGrath et al. 2001), which is the basis for the turnover time calculation of Okin et al. (2004).

An additional point of comparison is Hawaii, which receives a dust-derived P flux of 0.009 kg ha^{-1} $year^{-1}$ (Chadwick et al. 1999), $\sim$25 times lower than the dust-derived P flux calculated for the Rio Icacos watershed. A broad review of forest soil P contents undertaken by Johnson et al. (2003) indicates that Hawaiian oxisols generally have both greater total soil P content and greater labile soil P contents as compared to Luquillo Mountain soils (suggesting longer soil P turnover times). Despite the low dust fluxes and higher soil P content in Hawaii, ecosystem productivity at a 4.1 Ma site in Hawaii is controlled by dust-derived P (Chadwick et al. 1999). Inter-site differences in biota, disturbance regimes, erosion styles, soil mineralogy and soil hydrology inevitably play an important role in determining the dynamics of P cycling in various tropical ecosystems. However, at first order, this comparison supports the potentially important role of dust-derived P based simply on the larger dust-derived P flux and smaller soil P content in Luquillo Mountain ecosystems.

Conceptual models of P depletion

Multiple studies of soil and ecosystem chronosequences demonstrate progressive depletion of non-occluded or “available” soil P with increasing age (Crews et al. 1995; Wardle et al. 2004). However, several authors have argued that depletion of available P in older soils is restricted to stable tectonic settings and is unlikely to occur in settings of even moderate uplift and erosion (Porder et al. 2007; Vitousek et al. 2003; Wardle et al. 2004). It has been argued that the chronosequences that have been studied show P depletion in old soils in part because chronosequences are inherently focused on stable, undisturbed sites (Wardle et al. 2004). At the oldest end of the well-studied Hawaiian chronosequence, Vitousek et al. (2003) show that ecosystem P availability varies as much across an erosion gradient of 250 m (from a stable landscape position to an eroding hillslope) as it does over 4 Ma of soil and ecosystem development across stable landscape positions.

In the Luquillo Mountains, however, many soils exhibit depletion of available P despite active uplift and erosion rates of roughly 50 mm ka^{-1} (Scatena 1995). This occurs because the majority of P loss due to weathering occurs in saprock, at depths of between 2 and 24 m, while the majority of erosion occurs at shallower depths. The available soil P contents determined for Luquillo soils are similar to or lower than the values seen in the oldest soils of the Hawaiian (developed on basalt) and Franz Joseph (developed on greywacke glacial till in New Zealand) soil chronosequences of $\sim$1–4 mol m^{-3} (Porder et al. 2007). Frizano et al. (2002) analyzed soil P content in mature forest in the Rio Icacos area, and found available P content of 0.74 mol m^{-3}, based on the sum of resin P, bicarbonate extractable P, and NaOH extractable organic P (assuming that values for 0–60 cm depth interval are directly proportional to values for the 1 m depth interval). Similarly, a compilation of six different studies of soil chemistry around the Luquillo Mountains showed a range of available P concentrations of 6–26 μg g^{-1} based on bicarbonate extraction, which is equivalent to a range of 0.2–0.8 mol m^{-3} assuming soil density of 1 g cm^{-3} (Silver 1994). P depletion in Luquillo Mountain soils is also evident on the basis of the total soil P content. The average total soil P content in the Rio Icacos watershed of 0.011 ± 0.001% P ($n = 91$) (Riebe et al. 2003) plots at the low end of the range of total soil P content for humid tropical forests, which is between 0.005 and 0.2% P (Silver 1994).

Based on the expected age of Luquillo soils, their level of P depletion fits with the conceptual model of Porder et al. (2007) of the evolution of soil P availability with age as calibrated with data from the Franz Joseph chronosequence, but outpaces the model as calibrated with data from the Hawaiian basalt chronosequence. Considering the range of 2–24 m depth and dividing by a denudation velocity of 65 mm ka^{-1} indicates the likely range of regolith residence times (soil "age") in the Rio Icacos watershed is between 30 and 370 ka. On the other hand, in the model based on the well-studied Hawaiian soils, depletion of available P is only evident after 1,000 ka (although data are lacking to constrain the model between 150 ka and 1,400 ka). This indicates that in addition to age and erosion rate, variables such as lithology, soil hydrology, and weathering rates (which vary widely between Luquillo and Hawaii) are essential to any attempt to predict the evolution of soil P availability.

It is important to note that depletion of available soil P cannot simply be extended to the idea of ecosystem P limitation in the Luquillo Mountains because no studies in this region have clearly demonstrated widespread limitation by P or any other individual nutrient. However, in comparison with the Hawaiian and Franz Joseph chronosequence soils where P limitation has been reported (Porder et al. 2007), the low available P content of Luquillo soils suggests that P limitation in Luquillo ecosystems is a possibility. When considering the P budget on timescales of uplift and erosion (10^2–10^6 years), transformation of soil P to occluded forms should not necessarily be considered a loss from the system, based on evidence that multiple abiotic and biotic mechanisms can promote the availability of occluded phases to plants. By accounting for occluded P phases as irreversible losses from an ecosystem, the dependency of ecosystems on either uplift and erosion or atmospheric deposition will tend to be overestimated. Nevertheless, the work demonstrating P limitation in old Hawaiian soils with relatively large pools of occluded P suggests that the availability of occluded soil P (or the associated energetic costs to biomass of accessing occluded P) cannot be widely assumed (Vitousek and Farrington 1997).

Conclusions

A new Sr isotope-based dust deposition calculation for the Rio Icacos watershed in the Luquillo Mountains of Puerto Rico demonstrates the utility of geochemical tools in quantifying the biogeochemical relevance of dust deposition. Unlike direct atmospheric measurements, this approach provides long-term, spatially averaged fluxes, and allows dust-derived net P inputs to be distinguished from total atmospheric P inputs, which in turn allows the importance of the dust-derived P inputs to be evaluated relative to the rest of the P budget. Similar to findings from the older Hawaiian Islands (Chadwick et al. 1999), the magnitude of the dust-derived P flux (0.23 ± 0.08 kg ha^{-1} $year^{-1}$) in the Rio Icacos watershed appears to be large enough relative to other P fluxes to play an important role in the soil P budget.

The combined soil and biomass P pool turnover time, calculated as the pool size divided by the total inputs, is between 1.8 ka and 4.2 ka. Approximately half of the total inputs to soil-and-biomass P are derived from dust, and it would take between 2.8 ka and 7.0 ka for dust alone to supply the pool. The P nutrient dynamics presented here are deliberately conservative; first because the total soil P pool is considered as potentially important to the ecosystem, instead of only non-occluded forms, and second, because the depth of soil considered when defining the soil P pool is greater as compared to many analyses of P cycling at other sites. The soil P turnover time is shorter than the soil residence time (~15 ka), indicating that dust is a potentially important nutrient source in Luquillo Mountain ecosystems. In contrast to expectations regarding actively eroding systems, Luquillo Mountain soils exhibit relatively low available P pools (<1 mol P m^{-3} soil), due to the physical separation between the active weathering zone and the rooting zone. There is no clear consensus on nutrient limitation in the

Luquillo Mountains, but the input of mineral nutrients via dust is likely to play an important role in the biogeochemistry of these ecosystems.

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References

Artaxo P et al (1998) Large-scale aerosol source apportionment in Amazonia. J Geophys Res Atmos 103(D24):31837–31847. doi:10.1029/98JD02346

Avila A, Alarcon M, Queralt I (1998) The chemical composition of dust transported in red rains—its contribution to the biogeochemical cycle of a Holm oak forest in Catalonia (Spain). Atmos Environ 32(2):179–191. doi:10.1016/S1352-2310(97)00286-0

Baker AR, French M, Linge KL (2006a) Trends in aerosol nutrient solubility along a west-east transect of the Saharan dust plume. Geophys Res Lett 33(7):L07805

Baker AR, Jickells TD, Witt M, Linge KL (2006b) Trends in the solubility of iron, aluminium, manganese and phosphorus in aerosol collected over the Atlantic Ocean. Mar Chem 98(1):43–58. doi:10.1016/j.marchem.2005.06.004

Bergametti G, Gomes L, Coudegaussen G, Rognon P, Lecoustumer MN (1989) African dust observed over Canary Islands: source regions identification and transport pattern for some summer situations. J Geophys Res Atmos 94(D12):14855–14864. doi:10.1029/JD094iD12p14855

Bern CR, Townsend AR, Farmer GL (2005) Unexpected dominance of parent-material strontium in a tropical forest on highly weathered soils. Ecology 86(3):626–632. doi:10.1890/03-0766

Bhatt MP, McDowell WH (2007) Controls on major solutes within the drainage network of a rapidly weathering tropical watershed. Water Resour Res 43:W11402. doi:10.1029/2007WR005915

Biscaye PE, Chesselet R, Prospero JM (1974) Rb-Sr, 87Sr/86Sr isotope system as an index of provenance of continental dusts in the open Atlantic Ocean. J Rech Atmos 8:819–829

Brown S, Lugo AE, Silander S, Liegel L (1983) Research history and opportunities in the Luquillo Experimental Forest. USDA, Forest Service General Technical Report S0-44, Southern Forest Experiment Station, New Orleans, Louisiana

Brown ET, Stallard RF, Larsen MC, Raisbeck GM, Yiou F (1995) Denudation rates determined from the accumulation of in situ produced ^{10}Be in the Luquillo Experimental Forest, Puerto Rico. Earth Planet Sci Lett 129:193–202. doi:10.1016/0012-821X(94)00249-X

Bruijnzeel LA (1989) Nutrient content of bulk precipitation in south-central Java, Indonesia. J Trop Ecol 5:187–202

Bruijnzeel LA (1991) Nutrient input output budgets of tropical forest ecosystems: a review. J Trop Ecol 7:1–24

Buss HL, Sak PB, Webb SM, Brantley SL (2008) Weathering of the Rio Blanco quartz diorite, Luquillo Mountains, Puerto Rico: coupling oxidation, dissolution, and fracturing. Geochim Cosmochim Acta 72:4488–4507. doi:10.1016/j.gca.2008.06.020

Carbo P, Krom MD, Homoky WB, Benning LG, Herut B (2005) Impact of atmospheric deposition on N and P geochemistry in the southeastern Levantine basin. Deep Sea Res Part II Top Stud Oceanogr 52(22–23):3041–3053. doi:10.1016/j.dsr2.2005.08.014

Chacon N, Silver WL, Dubinsky EA, Cusack DF (2006) Iron reduction and soil phosphorus solubilization in humid tropical forests soils: the roles of labile carbon pools and an electron shuttle compound. Biogeochemistry 78(1):67–84. doi:10.1007/s10533-005-2343-3

Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO (1999) Changing sources of nutrients during four million years of ecosystem development. Nature 397(6719):491–497. doi:10.1038/17276

Chestnut TJ, Zarin DJ, McDowell WH, Keller M (1999) A nitrogen budget for late-successional hillslope tabonuco forest, Puerto Rico. Biogeochemistry 46(1–3):85–108. doi:10.1007/BF01007575

Cleveland CC, Reed SC, Townsend AR (2006) Nutrient regulation of organic matter decomposition in a tropical rain forest. Ecology 87(2):492–503. doi:10.1890/05-0525

Cox SB, Willig MR, Scatena FN (2002) Variation in nutrient characteristics of surface soils from the Luquillo Experimental Forest of Puerto Rico: a multivariate perspective. Plant Soil 247(2):189–198. doi:10.1023/A:1021488313783

Crews TE et al (1995) Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. Ecology 76(5):1407–1424. doi:10.2307/1938144

Cross AF, Schlesinger WH (1995) A literature review and evaluation of the Hedley fractionation: applications to the biogeochemical cycle of soil phosphorus in natural ecosystems. Geoderma 64(3–4):197–214. doi:10.1016/0016-7061(94)00023-4

Dalling JW, Tanner EVJ (1995) An experimental study of regeneration on landslides in montane rain forest in Jamaica. J Ecol 83(1):55–64. doi:10.2307/2261150

De Longe M, D'Odorico P, Lawrence D (2008) Feedbacks between phosphorus deposition and canopy cover: the emergence of multiple stable states in tropical dry forests. Glob Change Biol 14(1):154–160

Eijsink LM, Krom MD, Herut B (2000) Speciation and burial flux of phosphorus in the surface sediments of the Eastern Mediterranean. Am J Sci 300(6):483–503. doi:10.2475/ajs.300.6.483

Elser JJ et al (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135–1142. doi:10.1111/j.1461-0248.2007.01113.x

Fetcher N et al (1996) Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. J Ecol 84(3):331–341. doi:10.2307/2261196

Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the biosphere: integrating terrestrial

and oceanic components. Science 281(5374):237–240. doi:10.1126/science.281.5374.237
Filippelli GM, Souch C (1999) Effects of climate and landscape development on the terrestrial phosphorus cycle. Geology 27(2):171–174. doi:10.1130/0091-7613(1999)027≤0171:EOCALD≥2.3.CO;2
Fletcher RC, Buss HL, Brantley SL (2006) A spheroidal weathering model coupling porewater chemistry to soil thickness during steady-state denudation. Earth Planet Sci Lett 244:444–457. doi:10.1016/j.epsl.2006.01.055
Formenti P et al (2001) Saharan dust in Brazil and Suriname during the large-scale biosphere-atmosphere experiment in Amazonia (LBA)—cooperative LBA regional experiment (CLAIRE) in March 1998. J Geophys Res Atmos 106(D14):14919–14934. doi:10.1029/2000JD900827
Frizano J, Johnson AH, Vann DR, Scatena FN (2002) Soil phosphorus fractionation during forest development on landslide scars in the Luquillo Mountains, Puerto Rico. Biotropica 34(1):17–26
Galloway JN et al (2004) Nitrogen cycles: past, present, and future. Biogeochemistry 70(2):153–226. doi:10.1007/s10533-004-0370-0
Glaccum RA, Prospero JM (1980) Saharan aerosols over the tropical North Atlantic: mineralogy. Mar Geol 37(3–4):295–321. doi:10.1016/0025-3227(80)90107-3
Goudie AS, Middleton NJ (2001) Saharan dust storms: nature and consequences. Earth Sci Rev 56(1–4):179–204. doi:10.1016/S0012-8252(01)00067-8
Graham WF, Duce RA (1979) Atmospheric pathways of the phosphorus cycle. Geochim Cosmochim Acta 43(8):1195–1208. doi:10.1016/0016-7037(79)90112-1
Graham WF, Duce RA (1981) Atmospheric input of phosphorus to remote tropical islands. Pac Sci 35(3):241–255
Grousset FE, Biscaye PE, Zindler A, Prospero J, Chester R (1988) Neodymium isotopes as tracers in marine sediments and aerosols: North Atlantic. Earth Planet Sci Lett 87(4):367–378. doi:10.1016/0012-821X(88)90001-5
Grousset FE, Rognon P, Coudegaussen G, Pedemay P (1992) Origins of peri-Saharan dust deposits traced by their Nd and Sr isotopic composition. Palaeogeogr Palaeoclimatol Palaeoecol 93(3–4):203–212. doi:10.1016/0031-0182(92)90097-O
Grousset FE et al (1998) Saharan wind regimes traced by the Sr–Nd isotopic composition of subtropical Atlantic sediments: last glacial maximum vs today. Quat Sci Rev 17(4–5):395–409. doi:10.1016/S0277-3791(97)00048-6
Guariguata MR (1990) Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. J Ecol 78(3):814–832. doi:10.2307/2260901
Hamdan J, Burnham CP (1996) The contribution of nutrients from parent material in three deeply weathered soils of Peninsular Malaysia. Geoderma 74(3–4):219–233. doi:10.1016/S0016-7061(96)00062-6
Heartsill-Scalley T, Scatena FN, Estrada C, McDowell WH, Lugo AE (2007) Disturbance and long-term patterns of rainfall and throughfall nutrient fluxes in a subtropical wet forest in Puerto Rico. J Hydrol (Amst) 333(2–4):472–485. doi:10.1016/j.jhydrol.2006.09.019
Herbert DA, Fownes JH (1995) Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil. Biogeochemistry 29(3):223–235. doi:10.1007/BF02186049
Herut B, Zohary T, Robarts RD, Kress N (1999) Adsorption of dissolved phosphate onto loess particles in surface and deep Eastern Mediterranean water. Mar Chem 64(4):253–265. doi:10.1016/S0304-4203(98)00073-5
Herut B, Collier R, Krom MD (2002) The role of dust in supplying nitrogen and phosphorus to the Southeast Mediterranean. Limnol Oceanogr 47(3):870–878
Herwitz SR, Muhs DR, Prospero JM, Mahan S, Vaughn B (1996) Origin of Bermuda's clay-rich quaternary paleosols and their paleoclimatic significance. J Geophys Res Atmos 101(D18):23389–23400. doi:10.1029/96JD02333
Hicks BB, Wesely ML, Durham JL (1980) Critique of methods to measure dry deposition: workshop summary. U.S. Environmental Sciences Research Laboratory, Research Triangle Park, NC
Holmes CW, Miller R (2004) Atmospherically transported elements and deposition in the Southeastern United States: local or transoceanic? Appl Geochem 19(7):1189–1200. doi:10.1016/j.apgeochem.2004.01.015
Janos DP (1980) Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth. Ecology 61(1):151–162. doi:10.2307/1937165
Johnson AH, Frizano J, Vann DR (2003) Biogeochemical implications of labile phosphorus in forest soils determined by the Hedley fractionation procedure. Oecologia 135(4):487–499
Jordan CF (1985) Nutrient cycling in tropical forest ecosystems: principles and their application in management and conservation. Wiley, New York, p 190
Jordan C, Golley F, Hall J, Hall J (1980) Nutrient scavenging of rainfall by the canopy of an Amazonian rain forest. Biotropica 12(1):61–66. doi:10.2307/2387774
Kaspari M et al (2008) Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecol Lett 11(1):35–43
Kellman M, Hudson J, Sanmugadas K (1982) Temporal variability in atmospheric nutrient influx to a tropical ecosystem. Biotropica 14(1):1–9. doi:10.2307/2387753
Kohfeld KE, Harrison SP (2001) DIRTMAP: the geological record of dust. Earth Sci Rev 54(1–3):81–114. doi:10.1016/S0012-8252(01)00042-3
Kurtz AC, Derry LA, Chadwick OA (2001) Accretion of Asian dust to Hawaiian soils: isotopic, elemental, and mineral mass balances. Geochim Cosmochim Acta 65(12):1971–1983. doi:10.1016/S0016-7037(01)00575-0
Larsen MC (1997) Tropical geomorphology and geomorphic work: a study of geomorphic processes and sediment and water budgets in montane humid-tropical forested and developed watersheds, Puerto Rico. Ph.D. thesis, University of Colorado, 341 pp
Larsen MC, Parks JE (1997) How wide is a road? The association of roads and mass-wasting in a forested montane environment. Earth Surf Process Landf 22(9):835–848. doi:10.1002/(SICI)1096-9837(199709)22:9≤835::AID-ESP782≥3.0.CO;2-C
Larsen MC, Simon A (1993) A rainfall intensity-duration threshold for landslides in a humid tropical environment, Puerto-Rico. Geogr Ann Ser A 75(1–2):13–23
Larsen MC, Torres-Sanchez AJ (1992) Landslides triggered by the rainfall associated with Hurricane Hugo, 1989. Caribb J Sci 28(3–4):113–120

Larsen MC, Torres-Sanchez AJ, Concepcion IM (1999) Slopewash, surface runoff and fine-litter transport in forest and landslide scars in humid-tropical steeplands, Luquillo Experimental Forest, Puerto Rico. Earth Surf Process Landf 24(6):481–502. doi:10.1002/(SICI)1096-9837(199906)24:6≤481::AID-ESP967≥3.0.CO;2-G

Lawrence WT (1996) The Food Base. In: Reagan DP, Waide RB (eds) The food web of a tropical forest. University of Chicago Press, Chicago, p 616

Lesack LFW, Melack JM (1996) Mass balance of major solutes in a rainforest catchment in the Central Amazon: Implications for nutrient budgets in tropical rainforests. Biogeochemistry 32(2):115–142. doi:10.1007/BF00000355

Lindberg SE, Lovett GM (1985) Field measurements of particle dry deposition rates to foliage and inert surfaces in a forest canopy. Environ Sci Technol 19(3):238–244. doi:10.1021/es00133a003

Lindberg SE, Lovett GM, Schaefer DA, Bredemeier M (1988) Dry deposition velocities and surface-to-canopy scaling factors for aerosol calcium from forest canopy throughfall. J Aerosol Sci 19(7):1187–1190. doi:10.1016/0021-8502(88)90132-2

Lodge DJ, McDowell WH, McSwiney CP (1994) The importance of nutrient pulses in tropical forests. Trends Ecol Evol 9(10):384–387. doi:10.1016/0169-5347(94)90060-4

Lundgren L (1978) Studies of soil and vegetation development on fresh landslide scars in the Mgeta Valley, western Uluguru Mountains, Tanzania. Geogr Ann Ser A 60(3–4):91–127

Mahowald NM et al (2005a) Impacts of biomass burning emissions and land use change on Amazonian atmospheric phosphorus cycling and deposition. Global Biogeochemical Cycles 19(4):GB4030

Mahowald NM et al (2005b) Atmospheric global dust cycle and iron inputs to the ocean. Global Biogeochem Cycles 19(4):GB4025. doi:10.1029/2004GB002402

Mahowald NM et al (2006) Change in atmospheric mineral aerosols in response to climate: Last glacial period, preindustrial, modern, and doubled carbon dioxide climates. J Geophys Res Atmos 111(D10):D10202. doi:10.1029/2005JD006653

Mahowald N et al (2008) Global distribution of atmospheric phosphorus sources, concentrations and deposition rates, and anthropogenic impacts. Global Biogeochem Cycles 22(4). doi:10.1029/2008GB003240

Matson PM, McDowell WH, Townsend AR, Vitousek PM (1999) The globalization of N deposition: ecosystem consequences in tropical environments. Biogeochemistry 46:67–83

McDowell WH, Asbury CE (1994) Export of carbon, nitrogen, and major ions from three tropical montane watersheds. Limnol Oceanogr 39:111–125

McGrath DA, Smith CK, Gholz HL, Oliveira FD (2001) Effects of land-use change on soil nutrient dynamics in Amazonia. Ecosystems (NY, Print) 4(7):625–645. doi:10.1007/s10021-001-0033-0

McGroddy ME, Daufresne T, Hedin LO (2004) Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial redfield-type ratios. Ecology 85(9):2390–2401. doi:10.1890/03-0351

McTainsh G (1980) Harmattan dust deposition in Northern Nigeria. Nature 286(5773):587–588. doi:10.1038/286587a0

Miller HG, Miler JD (1980) Collection and retention of atmospheric pollutants by vegetation. In: International Conference on Ecological Impacts of Acid Precipitation, Sandefjord, Norway. SNSF Project Oslo, Norway

Moreno T et al (2006) Geochemical variations in aeolian mineral particles from the Sahara-Sahel Dust Corridor. Chemosphere 65(2):261–270. doi:10.1016/j.chemosphere.2006.02.052

Muhs DR, Bush CA, Stewart KC, Rowland TR, Crittenden RC (1990) Geochemical evidence of Saharan dust parent material for soils developed on Quaternary limestones of Caribbean and western Atlantic islands. Quat Res 33(2):157–177. doi:10.1016/0033-5894(90)90016-E

Muhs DR, Budahn JR, Prospero JM, Carey SN (2007) Geochemical evidence for African dust inputs to soils of western Atlantic islands: Barbados, the Bahamas, and Florida. J Geophys Res Atmos 112:F02009. doi:10.1029/2005JF000445

Myster RW, Fernandez DS (1995) Spatial gradients and patch structure on two Puerto Rican landslides. Biotropica 27(2):149–159. doi:10.2307/2388990

Neff JC, Reynolds RL, Belnap J, Lamothe P (2005) Multidecadal impacts of grazing on soil physical and biogeochemical properties in southeast Utah. Ecol Appl 15(1):87–95. doi:10.1890/04-0268

Neff JC et al (2008) Increasing eolian dust deposition in the western United States linked to human activity. Nat Geosci 1(3):189–195. doi:10.1038/ngeo133

Newman EI (1995) Phosphorus inputs to terrestrial ecosytems. J Ecol 83(4):713–726. doi:10.2307/2261638

Okin GS, Mahowald N, Chadwick OA, Artaxo P (2004) Impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems. Global Biogeochem Cycles 18(2). doi:10.1029/2003GB002145

Olander LP, Vitousek PM (2004) Biological and geochemical sinks for phosphorus in soil from a wet tropical forest. Ecosystems (NY, Print) 7(4):404–419. doi:10.1007/s10021-004-0264-y

Paoli GD, Curran LM (2007) Soil nutrients limit fine litter production and tree growth in mature lowland forest of Southwestern Borneo. Ecosystems (NY, Print) 10(3):503–518. doi:10.1007/s10021-007-9042-y

Paoli GD, Curran LM, Zak DR (2005) Phosphorus efficiency of Bornean rain forest productivity: evidence against the unimodal efficiency hypothesis. Ecology 86(6):1548–1561. doi:10.1890/04-1126

Peretyazhko T, Sposito G (2005) Iron(III) reduction and phosphorous solubilization in humid tropical forest soils. Geochim Cosmochim Acta 69(14):3643–3652. doi:10.1016/j.gca.2005.03.045

Perry KD, Cahill TA, Eldred RA, Dutcher DD, Gill TE (1997) Long-range transport of North African dust to the eastern United States. J Geophys Res Atmos 102(D10):11225–11238. doi:10.1029/97JD00260

Pett-Ridge JC, Derry LA, Kurtz AC (2009) Sr isotopes as a tracer of weathering processes and dust inputs in a tropical granitoid watershed, Luquillo Mountains, Puerto Rico. Geochim Cosmochim Acta 73:25–43. doi:10.1016/j.gca.2008.09.032

Porder S, Paytan A, Vitousek PM (2005) Erosion and landscape development affect plant nutrient status in the Hawaiian Islands. Oecologia 142(3):440–449. doi:10.1007/s00442-004-1743-8

Porder S, Vitousek PM, Chadwick OA, Chamberlain CP, Hilley GE (2007) Uplift, erosion, and phosphorus limitation in terrestrial ecosystems. Ecosystems (NY, Print) 10(1):158–170. doi:10.1007/s10021-006-9011-x

Proctor J (1987) Nutrient cycling in primary and old secondary rain forests. Appl Geogr 7(2):135–152. doi:10.1016/0143-6228(87)90046-4

Prospero JM, Lamb PJ (2003) African droughts and dust transport to the Caribbean: climate change implications. Science 302(5647):1024–1027. doi:10.1126/science.1089915

Prospero JM, Nees RT (1986) Impact of the North African drought and El-Nino on mineral dust in the Barbados trade winds. Nature 320(6064):735–738. doi:10.1038/320735a0

Prospero JM, Bonatti E, Schubert C, Carlson TN (1970) Dust in Caribbean atmosphere traced to an African dust storm. Earth Planet Sci Lett 9(3):287–293. doi:10.1016/0012-821X(70)90039-7

Prospero JM, Glaccum RA, Nees RT (1981) Atmospheric transport of soil dust from Africa to South America. Nature 289(5798):570–572. doi:10.1038/289570a0

Prospero JM, Nees RT, Uematsu M (1987) Deposition rate of particulate and dissolved aluminum derived from Saharan dust in precipitation at Miami, Florida. J Geophys Res Atmos 92(D12):14723–14731. doi:10.1029/JD092iD12p14723

Read DJ (1991) Mycorrhizas in ecosystems: nature's response to the "law of the minimum". In: Hawkins DL (ed) Frontiers in Mycology (honorary and general lectures from the Fourth Internantional Mycological Congress), Regensburg, 1990. CAB International, Wallingford

Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. Proc Natl Acad Sci USA 101(30):11001–11006. doi:10.1073/pnas.0403588101

Reid EA, Reid JS, Meier MM, Dunlap MR, Cliff SS, Broumass A, Perry K, Maring H (2003) Characterization of African dust transported to Puerto Rico by individual particle and size segregated bulk analysis. J Geophys Res Atmos 108(D19): 8591

Reynolds R, Neff J, Reheis M, Lamothe P (2006) Atmospheric dust in modem soil on aeolian sandstone, Colorado Plateau (USA): variation with landscape position and contribution to potential plant nutrients. Geoderma 130(1–2): 108–123. doi:10.1016/j.geoderma.2005.01.012

Richter DD, Allen HL, Li JW, Markewitz D, Raikes J (2006) Bioavailability of slowly cycling soil phosphorus: major restructuring of soil P fractions over four decades in an aggrading forest. Oecologia 150(2):259–271. doi:10.1007/s00442-006-0510-4

Ridame C, Guieu C (2002) Saharan input of phosphate to the oligotrophic water of the open western Mediterranean Sea. Limnol Oceanogr 47(3):856–869

Riebe CS, Kirchner JW, Finkel RC (2003) Long-term rates of chemical weathering and physical erosion from cosmogenic nuclides and geochemical mass balance. Geochim Cosmochim Acta 67(22):4411–4427. doi:10.1016/S0016-7037(03)00382-X

Rognon P, Coude-Gaussen G, Revel M, Grousset FE, Pedemay P (1996) Holocene Saharan dust deposition on the Cape Verde Islands: sedimentological and Nd–Sr isotopic evidence. Sedimentology 43:359–366. doi:10.1046/j.1365-3091.1996.d01-8.x

Sanchez PA (1976) Properties and management of soils in the tropics. Wiley, New York

Scatena FN (1995) Relative scales of time and effectiveness of watershed processes in a tropical Montane Rain Forest of Puerto Rico. In: Miller AJ, Potter KW, Wilcock PR (eds) Natural and anthropogenic influences in fluvial geomorphology. Geophysical Monographs, AGU, Washington, DC, pp 103–111

Scatena FN, Lugo AE (1995) Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico. Geomorphology 13(1–4):199–213. doi:10.1016/0169-555X(95)00021-V

Schulz MS, White AF (1999) Chemical weathering in a tropical watershed, Luquillo mountains, Puerto Rico III: quartz dissolution rates. Geochim Cosmochim Acta 63(3–4):337–350. doi:10.1016/S0016-7037(99)00056-3

Seiders VM (1974) Cretaceous and lower tertiary stratigraphy of the Gurabo and El Yunque Quadrangles, Puerto Rico. U. S. Geological Survey, Washington, DC, Bulletin F 1294

Sharpley AN, Tiessen H, Cole CV (1987) Soil phosphorus forms extracted by soil tests as a function of pedogenesis. Soil Sci Soc Am J 51(2):362–365

Silver WL (1994) Is nutrient availability related to plant nutrient use in humid tropical forests? Oecologia 98(3–4): 336–343. doi:10.1007/BF00324222

Silver WL, Scatena FN, Johnson AH, Siccama TG, Sanchez MJ (1994) Nutrient availability in a montane wet tropical forest: spatial patterns and methodological considerations. Plant Soil 164(1):129–145. doi:10.1007/BF00010118

Silver WL, Lugo AE, Keller M (1999) Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. Biogeochemistry 44(3):301–328

Simon A, Larsen MC, Hupp CR (1990) The role of soil processes in determining mechanisms of slope failure and hillslope development in a humid-tropical forest, eastern Puerto Rico. Geomorphology 3(3/4):263–286. doi:10.1016/0169-555X(90)90007-D

Singer A, Dultz S, Argaman E (2004) Properties of the non-soluble fractions of suspended dust over the Dead Sea. Atmos Environ 38(12):1745–1753. doi:10.1016/j.atmosenv.2003.12.026

Smith AL, Schellekens JH, Diaz ALM (1998) Batholiths as markers of tectonic change in northeastern Caribbean. In: Lidiak E.G., Larue DK (eds) Tectonics and geochemistry of the northeastern Caribbean. Geological society of America special paper. Boulder, Colorado, pp 99–122

Soderberg K, Compton JS (2007) Dust as a nutrient source for fynbos ecosystems, South Africa. Ecosystems (NY, Print) 10(4):550–561. doi:10.1007/s10021-007-9032-0

Stoorvogel JJ, Van Breemen N, Janssen BH (1997) The nutrient input by Harmattan dust to a forest ecosystem in

Cote d'Ivoire, Africa. Biogeochemistry 37(2):145–157. doi:10.1023/A:1005734225727

Swap R, Garstang M, Greco S, Talbot R, Kallberg P (1992) Saharan dust in the Amazon Basin. Tellus B Chem Phys Meterol 44(2):133–149. doi:10.1034/j.1600-0889.1992.t01-1-00005.x

Tanner EVJ, Kapos V, Freskos S, Healey JR, Theobald AM (1990) Nitrogen and phosphorus fertilization of Jamaican montane forest trees. J Trop Ecol 6:231–238

Tanner EVJ, Kapos V, Franco W (1992) Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. Ecology 73(1):78–86. doi:10.2307/1938722

Tanner EVJ, Vitousek PM, Cuevas E (1998) Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. Ecology 79(1):10–22

Tiessen H, Stewart JWB, Cole CV (1984) Pathways of phosphorus transformations in soils of differing pedogenesis. Soil Sci Soc Am J 48(4):853–858

Townsend AR, Cleveland CC, Asner GP, Bustamante MMC (2007) Controls over foliar N:P ratios in tropical rain forests. Ecology 88(1):107–118. doi:10.1890/0012-9658(2007)88[107:COFNRI]2.0.CO;2

Tsukuda S, Sugiyama M, Harita Y, Nishimura K (2006) Atmospheric phosphorus deposition in Ashiu, Central Japan—source apportionment for the estimation of true input to a terrestrial ecosystem. Biogeochemistry 77(1):117–138. doi:10.1007/s10533-005-1943-2

Turner BF, Stallard RF, Brantley SL (2003) Investigation of in situ weathering of quartz diorite bedrock in the Rio Icacos basin, Luquillo Experimental Forest, Puerto Rico. Chem Geol 202(3–4):313–341. doi:10.1016/j.chemgeo.2003.05.001

USDA NRCS (2002) Soil Survey of Caribbean National Forest and Luquillo Experimental Forest, Commonwealth of Puerto Rico. USDA Natural Resources Conservation Service, Washington, DC

Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65(1):285–298. doi:10.2307/1939481

Vitousek PM, Farrington H (1997) Nutrient limitation and soil development: experimental test of a biogeochemical theory. Biogeochemistry 37(1):63–75. doi:10.1023/A:1005757218475

Vitousek PM, Sanford RL (1986) Nutrient cycling in moist tropical forest. Annu Rev Ecol Syst 17:137–167. doi:10.1146/annurev.es.17.110186.001033

Vitousek P et al (2003) Erosion and the rejuvenation of weathering-derived nutrient supply in an old tropical landscape. Ecosystems (NY, Print) 6(8):762–772. doi:10.1007/s10021-003-0199-8

Vogt KA et al (1993) Belowground responses as indicators of environmental change. Environ Exp Bot 33(1):189–205. doi:10.1016/0098-8472(93)90065-N

Walker TW, Syers JK (1976) Fate of phosphorus during pedogenesis. Geoderma 15(1):1–19. doi:10.1016/0016-7061(76)90066-5

Wardle DA, Walker LR, Bardgett RD (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. Science 305(5683):509–513. doi:10.1126/science.1098778

Weaver PL, Murphy PG (1990) Forest structure and productivity in Puerto Rico's Luquillo Mountains. Biotropica 22(1):69–82. doi:10.2307/2388721

Went FW, Stark N (1968) Mycorrhiza. Bioscience 18(11):1035–1039. doi:10.2307/1294552

White EJ, Turner F (1970) Method of estimating income of nutrients in a catch of airborne particles by a woodland canopy. J Appl Ecol 7(3):441–461. doi:10.2307/2401970

White AF et al (1998) Chemical weathering in a tropical watershed, Luquillo Mountains, Puerto Rico: I. Long-term versus short-term weathering fluxes. Geochim Cosmochim Acta 62(2):209–226. doi:10.1016/S0016-7037(97)00335-9

Whitmore TC (1989) Tropical forest nutrients, where do we stand? A tour de horizon. In: Proctor J (ed) Mineral Nutrients in tropical forest and savanna ecosystems. Blackwell Scientific Press, Oxford, pp 1–13

Wilcke W et al (2003) Soil properties on a chronosequence of landslides in montane rain forest, Ecuador. Catena 53(1):79–95. doi:10.1016/S0341-8162(02)00196-0

Wilke BM, Duke BJ, Jimoh WLO (1984) Mineralogy and chemistry of Harmattan dust in Northern Nigeria. Catena 11(1):91–96. doi:10.1016/S0341-8162(84)80009-0

Zarin DJ, Johnson AH (1995) Nutrient accumulation during primary succession in a montane tropical forest, Puerto Rico. Soil Sci Soc Am J 59(5):1444–1452