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Soil Phosphorus Fractionation during Forest Development on Landslide Scars in the Luquillo Mountains, Puerto Rico[1]

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ABSTRACT

Mineral soils from a chronosequence of landslide scars ranging in age from 1 to more than 55 years in a subtropical montane rain forest of eastern Puerto Rico were used to determine the rate at which labile P capital recovers during primary succession. Nine organic and inorganic soil P fractions were measured using the Hedley sequential extraction procedure. Deep soil cores (9 m) from a nearby site were also analyzed to determine the distribution of P fractions below the solum. Litterfall P was measured for two years in the landslide scars to estimate allochthonous litter P inputs, and published precipitation data were used to estimate annual atmospheric inputs of P to the recovering forests. In the upper solum (0–10 cm), organic matter increased with landslide age, as did resin-Pi, labile P (defined here as resin-Pi + HCO_3–Pi + HCO_3–Po) and total organic P. Occluded P decreased with increasing landslide age. No significant changes in P concentrations or pools were observed in 10 to 35 or in 35 to 60 cm depth intervals across the chronosequence. Labile soil P increased to approximately two-thirds of the pre-disturbance levels in the oldest landslide scar (>55 yr). Thus, plants, their associated microflora/fauna, and P inputs from off-site substantially altered the distribution of soil P fractions during forest recovery. Across the chronosequence, the increase in labile P accumulated in soil and biomass appeared to be greater than the estimated allochthonous inputs from litter and precipitation, indicating that as the forest developed, some occluded P may have been released for use by soil biota. Resin-Pi and labile P were correlated with soil organic matter content, suggesting, as in other highly weathered soils, organic matter accumulation and turnover are important in maintaining labile P pools. Primary mineral P (apatite) was scarce, even in deep soil cores.

Key words: *Caribbean; landslide scars; phosphorus availability; phosphorus fractionation; primary succession; Puerto Rico; soil phosphorus; tropical soils.*

Landslides result in relatively rapid turnover of the landscape in the montane forests of Puerto Rico (Scatena 1989). Regeneration of forests on landslide scars affords an opportunity to explore how forest vegetation and its associated microbes accumulate and manage reservoirs of nutrient capital in the subtropical wet forests and montane rain forests of this area. Zarin and Johnson (1995a, b) documented the rates at which above- and belowground pools of several nutrients recovered during afforestation of landslide scars in the palo colorado (*Cyrilla racemiflora*-dominated) forest zone of the Luquillo Experimental Forest, Puerto Rico (LEF). In soils sampled from a chronosequence of landslide scars, neutral-salt-extractable Ca, Mg, K, and total soil N pools recovered to pre-landslide levels in less than a century. Extractable inorganic P present in the soil of recent landslide scars was undetectable when measured using a modified Bray extraction, and given detection limits, not sufficient to grow another forest (Zarin & Johnson 1995a). Those results suggested that, as at other tropical sites (Dalling 1994, Tiessen *et al.* 1994, Fetcher *et al.* 1996), P may control the rate of biomass accumulation on landslides in the LEF. We reasoned that reestablishment of P capital after landslides could result from any of several sources: weathering of primary mineral P (*e.g.,* apatite present in the saprolite or underlying plutonic and volcanic rocks); P deposition in precipitation and dust; litter inputs from the surrounding forest; and through mycorrhizal intermediaries that dissolve tightly bound and otherwise sparingly soluble Al–P, Fe–P, and occluded P (*i.e.,* P buried within secondary minerals). Although the latter forms of P are considered unavailable to plants in the short term, research on mycorrhizal P uptake suggests that the fungi are indeed able to acquire non-labile forms

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of P bound in minerals (Cumming & Weinstein 1990, Read 1991, Paul & Clark 1996), and over the span of decades, this pool could be an important source of P for plants and their microbial associates.

The primary goals of this study were to determine the rate at which soil supplies of labile P (assumed to be related to plant-available P) accumulated under recovering forests and to identify sources of P that were quantitatively important in reestablishing labile P capital. We used the sequential extraction procedure of Tiessen and Moir (1993), modified from Hedley *et al.* (1982), to measure soil P fractions. Figure 1 shows how Tiessen *et al.* (1984) categorize soil P pools, the rapid or slow transfers among those pools, and the correspondence between those conceptual P pools and the P measured in the sequential fraction procedure. For the landslide chronosequence, the left side of Figure 1 represents relatively slow geochemical processes whereby primary mineral P in the underlying plutonic and volcanic rocks was transformed into secondary mineral P and occluded P over the 50,000 years estimated to produce the 10 m or so of weathered residuum that sits atop the bedrock (Scatena 1995). The middle of Figure 1 shows more labile pools of P that are relevant to short-term forest P cycling, and the right side of Figure 1 shows a pool of chemically and physically protected P that accumulates in recalcitrant organic matter as the soils and forest age.

A widely applicable relationship between chemically extracted P fractions and P availability to forest vegetation does not exist. There is general agreement, however, that inorganic P released to anion exchange resin and inorganic and organic P released to the $NaHCO_3$ solution (designated here as resin-Pi, HCO_3–Pi, and HCO_3–Po, respectively) are the most labile fractions, and are probably available to plants "in the short term" (*sensu* Cross & Schlesinger 1995). Phosphorus released by somewhat more aggressive extractants (NaOH–Pi, NaOH–Po, and dilute HCl–Pi) may be available to plants on a slightly longer time frame. In general, P released by the most aggressive extractants (hot concentrated HCl–Pi and –Po, and "residual P" determined by H_2SO_4 + H_2O_2 digestion) is considered unavailable to plants in the short term (Tiessen & Moir 1993, Cross & Schlesinger 1995). Accordingly, we focus primarily on the most labile P forms, resin-Pi, HCO_3–Pi, and HCO_3–Po as those that are most important for determining P available to plants in the short term.

MATERIALS AND METHODS

Study area.—The Luquillo Experimental Forest (LEF), administered by the U.S. Forest Service, includes 11,300 ha of moist, wet, and montane rain forests (*sensu* Holdridge 1967) in eastern Puerto Rico. The LEF is an area of high relief with elevations ranging from 200 to 1300 m. The topography is rugged and slopes are highly dissected. Slopes range from 10 to 100 percent (Larsen & Torres Sánchez 1992). The geology of the LEF consists of Lower Cretaceous marine volcaniclastic sandstone, mudstone, breccia, and conglomerate, intruded by a Tertiary-age quartz–diorite pluton called the Rio Blanco Stock (Seiders 1971). Saprolite overlies the bedrock with an average depth of *ca* 11 m. The highly leached soils formed from the saprolite are Oxisols, Ultisols, and Inceptisols, which are moderately plastic, moderately drained, highly weathered clays and clay loams with an average solum thickness of *ca* 1 m.

Landslides occur during and after large rainfall events, especially hurricanes. For example, Hurricane Hugo, which struck eastern Puerto Rico in 1989, caused hundreds of small landslides (Scatena & Larsen 1991, Larsen & Torres Sánchez 1992). Zarin (1993) located the plots used for this chronosequence study by analyzing USGS maps and original aerial photographs dating back to 1936. Five areas were selected to represent four discrete landslide age classes: 1986–1991, 1972–1979, 1951–1964, and pre-1936. Landslide scars ranging from 150 to 1000 m^2 in area were used as sampling units. Soil samples were obtained from elevations of 600 to 800 m, where mean annual rainfall ranges from 3000 to 4000 mm and mean annual temperature is *ca* 21°C (Brown *et al.* 1983, Zarin 1993). Slopes on these concave features range from 30 to more than 100 percent. Vegetation on the most recent landslides is very sparse, consisting mainly of mosses and isolated seedlings. Within 25 years, these landslides become covered with ferns, and seedlings and saplings that represent the mature forest. *Cyrilla racemiflora*, *Prestoa montana*, and *Micropholis chrysophylloides* are the most abundant tree species. Additional plots from the mature, *Cyrilla*-dominated forest (CDF) growing on slopes adjacent to the landslide plots were selected to represent a late-successional vegetation association consistent with the floristic trajectories of the younger plots.

Sampling design.—We used remaining soil from one set of Zarin's (1993) landslides supplemented

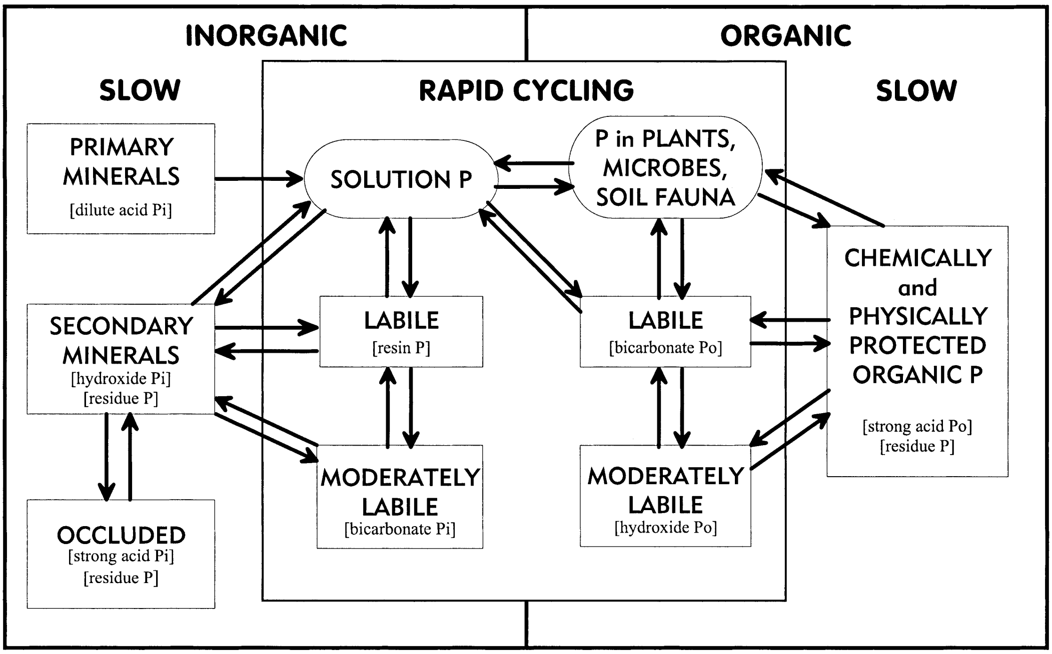

FIGURE 1. Conceptual model of soil P transformations with the measurable fractions in brackets (after Tiessen *et al.* 1984).

with randomly located samples collected from the same slides. The sites were located essentially adjacent to one another at 600 to 800 m elevation on material weathered from quartz diorite. Three random samples were used from each of the 0–10, 10–35, and 35–60 cm depths on landslides of four age classes: 1986–1991 (N = 1), 1972–1979 (N = 1), 1951–1964 (N = 2), and pre-1936 (N = 1). As a measure of steady-state forest conditions, soils were sampled at the same depths from one of Zarin's (1993) CDF plots adjacent to the set of landslides. Zarin (1993) estimated that this stand was *ca* 300 years old, based on tree diameters and local diameter growth rates.

Deep (to 9 m) core samples were obtained by the USDA Forest Service's International Institute of Tropical Forestry Laboratory. The samples were collected in stabilized landslide scars in the Bisley watershed, 15 km to the north and 300 m lower in elevation. These soils were weathered from volcaniclastic rocks, which are different in mineralogy but similar in overall chemical composition to the quartz diorite that underlies the sampled landslides.

Bulk litterfall was collected once a month for two years using six basket-type collectors deployed randomly on each of eight different landslide scars in the four age classes. We used the data collected from the most recent slides to assess the potential for litter input from off-site sources. Litterfall P data were also used as part of the calculated annual P requirement for the older stands.

Analytical procedures for soils and litter.—Soil samples were air-dried, manually cleared of fine roots, and ground to less than 40 mesh. P fractionation followed the procedure of Hedley *et al.* (1982) as modified by Tiessen and Moir (1993). This fractionation procedure separates P pools according to the aggressiveness of acidic and basic extractants used to remove progressively more P. Although the relationship between those chemically extracted fractions and P availability to forest vegetation is neither well established nor constant across soils, there is general agreement that the resin- and bicarbonate-extractable P fractions represent the P that is the most available to vegetation in the short term (Tiessen *et al.* 1984, Sparling *et al.* 1985, Tiessen & Moir 1993, Cross & Schlesinger 1995). We refer to the resin- and bicarbonate-extractable P as "labile P," and following the consensus, consider those to be the fractions that contribute to "plant-available P" in "the short term." Resin-P was extracted using a polymeric resin anion exchange membrane (BDH Laboratories ID. no. 5516400; HCO_3 saturated).

The Tiessen and Moir (1993) fractionation gives reasonably good replication between laboratories (Thomas 1996) and provides accurate results when the fractions are summed and compared to total P of a reference soil. Canadian Certified Reference Materials Project reference soil SO-4 was processed along with the landslide samples as a check on analytical accuracy. For total P, the recovery (the sum of all P fractions) was 101.5 ± 1.9 percent ($N = 12$) of the reference value. Quantities of soil P were calculated on a kg/ha basis using bulk densities reported for each site by Zarin (1993).

Bulk litter samples were oven-dried at 60°C and the dry weight measured. Samples were then ground to smaller than 20 mesh, homogenized, ashed in a furnace at 475°C overnight, and acid-digested using 5 N HCl for chemical analysis. C and N contents of all soil and litter samples were measured using a Carlo Erba elemental analyzer and standard operating procedures (Fisons Instruments NA1500, Dearborn, Michigan). Soils were sufficiently acidic to preclude the presence of inorganic carbonate (Zarin 1993). For the litter analyses, National Institute of Standards and Technology (NIST) citrus leaves (SRM 1572) and pine needles (SRM 1575) were included with field samples and served as internal references. Values determined for elemental concentrations of NIST samples were consistently within ±5 percent of published reference values (Trahey 1992).

STATISTICS.—A two-way ANOVA was used to test for effects of depth and time on soil P fractions, with $\log_{10}$ transforms as required to normalize the data. For the occluded P fraction, a two-way ranked means ANOVA was used, since those data could not be readily normalized. Changes in soil P pools with time occurred in the top 10 cm of soil, and we tested for age-related differences among sites using Tukey's multiple comparison test for normalized data and Dunn's multiple comparison test for the ranked occluded P data. Pearson product–moment correlations and simple linear regression analysis were used to assess relationships among soil P pools, and between soil P pools and organic C. The annual vegetation P requirement was estimated from the chronosequence data of Zarin (1993), for which it was assumed that the biological requirement was equal to the average annual biomass P increment (increased foliar, stem, and root biomass) plus P in annual litterfall.

RESULTS

PHOSPHORUS CONCENTRATIONS DURING SUCCESSION.—Mean values for percentages of total C and N and concentrations of extractable P fractions (µg/g) for the three depths (0–10, 10–35, and 35–60 cm) are reported in Table 1. Over time (representing the length of time plants had been growing on the sites) there were significant increases in organic C, resin-Pi, NaOH–Po, labile P, and the total organic P pool in the 0–10 cm depth increment ($P < 0.05$). In addition there was a significant reduction of the occluded P pool in the 0–10 cm depth increment. There were no statistically significant differences attributable to time in those fractions at other depths. Figure 2 illustrates the changes in P concentrations in the 0–10 cm depth increment over time, expressed as percentages of the total P present.

Soil N and C content declines with depth ($P < 0.001$), irrespective of landslide age. Differences with depth for the P fractions only occurred between the 0–10 cm and the two deeper 10–35 and 35–60 cm depth intervals ($P < 0.001$); there was no difference between the lower two depth intervals. When each age group was examined separately, there were no differences with depth in the newer landslide sites (1986–1991 and 1972–1979 sites), rather only in the older sites (1951–1964, pre-1936, and the mature CDF site; $P < 0.001$).

There was a trend of increasing organic P with increasing landslide age; organic P fractions (HCO_3–Po + NaOH–Po + concentrated HCl–Po) increased to *ca* 50 percent of the total P pool. Labile HCO_3–Po made up a small percentage of the total organic P pool (4% of total organic P on average); the remaining Po was found in the more stable organic forms (NaOH–Po and concentrated HCl–Po).

Soil C accounted for a majority of the variation in both resin-Pi and labile P concentrations (R^2 = 0.67 and 0.75, respectively; $P < 0.01$; Fig. 3). When labile P fractions within each landslide age class were regressed against soil C separately, the highest R^2 value occurred in the mature forest. Soil C reliably predicted the P concentration in each of the plant-available P fractions: labile P (R^2 = 0.90), resin-Pi (R^2 = 0.83), and HCO_3–Po (R^2 = 0.72; all $P < 0.001$).

SOIL P AMOUNTS.—Using the soil P concentrations and bulk density values from Zarin (1993), we estimated quantities of the soil P fractions on a per hectare basis (Table 2). For labile P and resin-Pi,

TABLE 1. *Soil nutrient concentrations from a chronosequence of landslide scars (<5 to >55 yr in age) and a mature forest (CDF*; ca 300 years old) in the Luquillo Experimental Forest, Puerto Rico. Values presented are means with standard errors in parentheses. For C, N, and the P fractions,* N = 3 *samples per depth for all sites, except at the 1986–1991 site,* N = 2 *in the 0–10 cm depth interval; at the 1951–1964 site,* N = 4 *in the 0–10 and 35–60 cm depth intervals and* N = 5 *in the 10–35 cm depth interval. P concentration units are in μg/g.*

Plot age	Depth (cm)	N (%)	C (%)	Resin-Pi	NaHCO$_3$– Pi	NaHCO$_3$– Po	NaOH– Pi	NaOH– Po	Dil. HCl–Pi	Conc. HCl– Pi	Conc. HCl– Po	Residue P	Total P
1986–1991	0–10	0.034	0.28	1.11	<0.04	0.22	11.20	4.39	2.60	124	2.97	18.2	162
			(0.62)	(0.96)	(<0.04)		(0.53)	(2.75)	(0.62)	(18.9)	(2.03)	(2.15)	(23.1)
	10–35	0.026	0.13	0.99	<0.04	<0.04	8.61	6.26	1.71	139	0.240	23.6	165
		(0.001)	(0.014)	(0.48)	(<0.04)	(<0.04)	(0.20)	(1.26)	(0.86)	(23.6)	(0.14)	(3.20)	(15.6)
	35–60	0.017	0.07	1.05	<0.04	<0.04	9.90	6.55	2.08	151	8.10	17.0	181
		(0.009)	(0.015)	(0.20)	(<0.04)	(<0.04)	(0.33)	(0.99)	(0.94)	(27.9)	(1.44)	(1.40)	(40.6)
1972–1979	0–10	0.05	0.72	1.45	0.33	1.43	5.83	16.0	4.64	94.6	2.90	20.3	146
		(0.006)	(0.08)	(0.82)	(0.33)	(1.15)	(3.00)	(6.90)	(1.70)	(4.40)	(1.10)	(0.20)	(5.20)
	10–35	0.03	0.19	0.86	<0.04	<0.04	13.6	8.62	3.33	82.5	2.10	21.1	119
		(0.001)	(0.05)	(0.86)	(<0.04)	(<0.04)	(1.90)	(4.20)	(0.20)	(11.70)	(0.30)	(0.90)	(11.6)
	35–60	0.008	0.07	1.31	<0.04	<0.04	8.71	3.75	4.05	75.6	2.80	17.8	111
		(0.008)	(0.02)	(0.71)	(<0.04)	(<0.04)	(0.24)	(1.40)	(0.60)	(5.00)	(0.90)	(2.10)	(4.10)
1951	0–10	0.13	2.32	9.50	1.40	3.30	17.2	49.0	9.60	147	17.8	42.2	292
		(0.01)	(0.24)	(2.80)	(0.69)	(1.40)	(11.9)	(15.5)	(3.90)	(43.0)	(13.6)	(6.00)	(25.1)
	10–35	0.08	1.00	3.10	0.70	0.09	16.9	30.1	4.40	104	20.7	35.5	208
		(0.02)	(0.25)	(0.80)	(0.40)	(0.06)	(7.90)	(18.1)	(2.00)	(26.6)	(11.6)	(3.00)	(21.5)
	35–60	0.05	0.48	1.54	0.20	0.88	28.3	7.35	4.70	131	16.8	35.1	212
		(0.01)	(0.16)	(0.69)	(0.05)	(0.50)	(6.60)	(2.30)	(0.80)	(34.0)	(14.2)	(4.60)	(22.0)
Pre-1936	0–10	0.16	1.80	2.12	1.12	2.40	16.8	22.8	0.64	26.8	7.85	20.0	100
		(0.02)	(0.40)	(0.30)	(0.40)	(1.70)	(0.40)	(3.60)	(0.20)	(1.50)	(2.30)	(1.50)	(1.70)
	10–35	0.12	1.33	2.22	0.52	1.19	28.5	23.2	3.24	33.7	4.76	26.0	123
		(0.02)	(0.30)	(1.20)	(0.52)	(0.50)	(13.8)	(6.90)	(0.50)	(8.90)	(0.50)	(6.50)	(36.0)
	35–60	0.05	0.42	0.96	<0.04	1.14	9.70	4.92	3.07	33.9	35.3	18.07	105
		(0.02)	(0.20)	(0.40)	(<0.04)	(1.14)	(0.70)	(2.50)	(1.10)	(11.0)	(33.0)	(1.80)	(22.0)
CDF	0–10	0.27	4.22	15.4	0.91	5.16	4.15	59.8	0.50	26.6	10.9	25.3	149
		(0.01)	(0.14)	(2.40)	(0.91)	(1.40)	(4.15)	(3.90)	(0.37)	(3.30)	(1.90)	(2.40)	(14.3)
	10–35	0.12	1.27	3.09	0.14	0.52	18.1	11.9	0.31	22.9	3.09	25.0	83.1
		(0.001)	(0.03)	(0.73)	(0.14)	(0.52)	(2.10)	(0.68)	(0.27)	(1.20)	(0.90)	(1.20)	(4.70)
	35–60	0.08	0.82	1.85	0.76	0.57	14.5	4.80	1.22	27.0	2.92	21.0	72.9
		(0.006)	(0.08)	(0.94)	(0.76)	(0.57)	(4.60)	(1.30)	(0.19)	(4.40)	(0.50)	(0.60)	(2.80)

* *Cyrilla*-dominated forest.

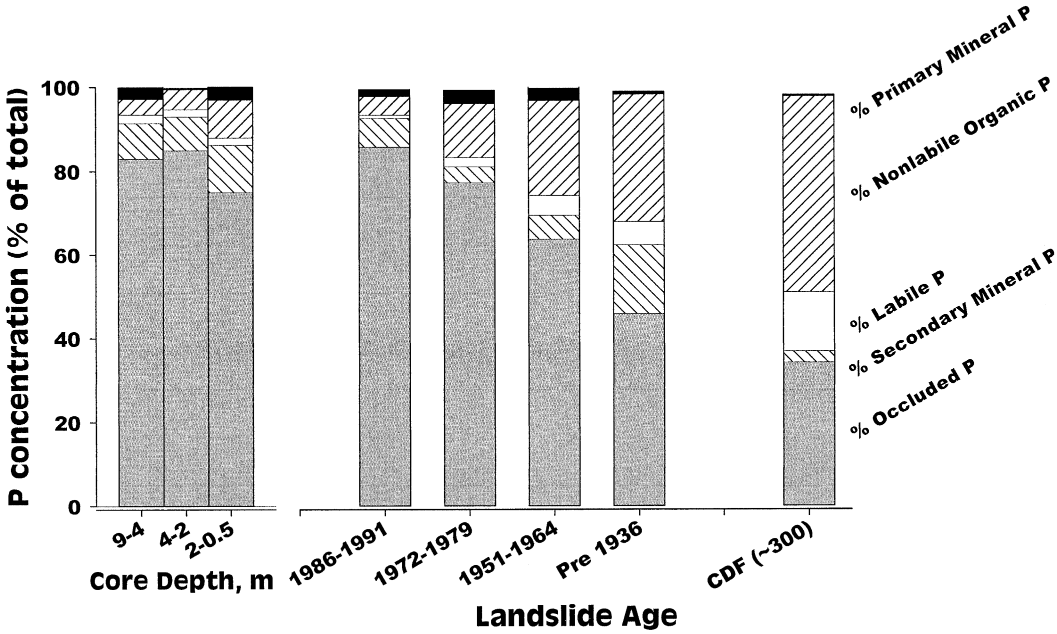

FIGURE 2. Percent P by fraction in deep soil cores and in landslides of differing ages.

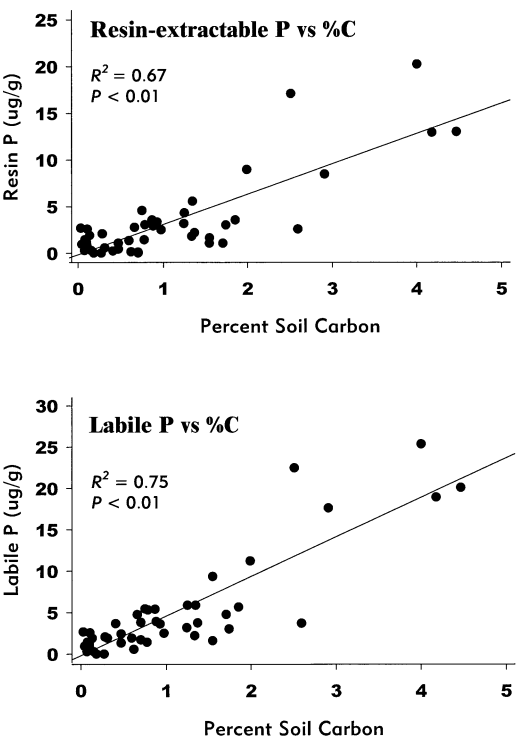

FIGURE 3. Relationship between landslide percent soil C and the resin-P and labile P pools.

there were significant trends toward increasing amounts in the 0–10 cm layer with increasing age ($P < 0.05$). Generally, total P showed a decreasing trend over time (not significant at $P < 0.05$).

Phosphorus concentrations in deep soil cores.—Deep core samples showed no changes in P fractionation with depth (Fig. 2), and the distribution of P fractions was indistinguishable from that in the recent landslide scars. The organic P fractions and labile P fractions remained fairly constant and at low levels throughout the 9 m profile. We found significant ($P < 0.01$) correlations between resin-Pi and HCO_3–Pi (Pearson product–moment $r = 0.90$) and between HCO_3–Pi and dilute HCl–P ($r = 0.65$). This suggests that inorganic fractions and processes dominate in maintaining the small labile P pools below the root zone.

Phosphorus inputs and requirements.—Across the set of landslide scars used for litter collection, amounts of litter and total litter P increased with increasing age. The average P input values, listed in Table 3, range from 0.58 kg/ha/yr in the 1986–1991 slides to 1.59 kg/ha/yr in the mature CDF.

Separating litter generated on-site from that originating off-site for the purposes of this study was not possible. In order to estimate P inputs

TABLE 2. *Phosphorus pool sizes (kg/ha) for 0–60 cm depth on LEF landslides. Values are means of two to five samples at each of three depths per landslide.*

	Labile P						Occluded P			
	Resin	HCO_3–		NaOH–		Dilute	Conc. HCl–		Residue	Total
Age	P	Pi	Po	Pi	Po	HCl–Pi	Pi	Po	P	P
1986–1991	5.6	0.0	0.5	77.0	49.6	17.6	1277	47.0	169	1640
1972–1979	10.7	0.0	2.0	46.8	58.4	26.9	624	18.4	145	932
1951–1964	19.0	4.0	6.1	171	134	38.2	924	77.2	236	1120
Pre-1936	12.4	5.8	7.0	142	110	22.0	219	176	153	847
CDF	28.2	4.8	8.7	123	95.2	6.22	195	27.9	173	662

from off-site litter over several decades of soil and forest development, we assumed that (1) when the canopy P content of a regrowing forest matched that of the surrounding forest, allochthonous litter P input to the site would be equal to litter output across the landslide boundary, and (2) net litter P inputs to landslide scars would decrease linearly as the forest regrew.

Zarin and Johnson (1995a) showed that canopy P content increases up to the age of the oldest slides (>55 yr), which we arbitrarily assigned an age of 70 years. We estimated off-site litter P inputs in year one to be 0.58 kg/ha/yr, the average value obtained from litter collected in litter traps on the most recent landslides (which was completely derived from off-site vegetation). With the assumption that net allochthonous litter deposition decreased linearly to zero in year 70 when litter input equals litter output across the slide boundary, our resulting estimates for allochthonous litter input to the recovering landslide scars was 20.3 kg/ha over the 70 years represented by the successional stands.

We used litterfall P data in conjunction with average rates of P accumulation in biomass determined by Zarin and Johnson (1995a) to estimate annual P requirement. Net accumulation of P in aggrading wood, foliage, and roots was less than 1 kg/ha/yr and foliar P turnover was less than 2 kg/ha/yr. Using these values, we estimated annual P requirement at less than 3 kg/ha/yr. For the mature CDF, this was considerably less than the pool of labile P in the soil (*ca* 41 kg/ha; Table 2).

McDowell and Asbury (1994) reported precipitation inputs to the Rio Icacos watershed where the study landslides are located. Extrapolating those data to 70 years of forest regrowth, total P inputs from precipitation were 21 kg/ha. Figure 4 summarizes the mass balance calculations of litter and precipitation inputs compared to the accumulation of labile soil P and P in live biomass. In the case of the CDF, biomass and labile soil P capital were not very different from those quantities in the 70-year-old forest. While it is difficult to estimate inputs from off-site for the oldest stand, we can put limits on such inputs if we assume that Zarin's (1993) estimate of 300 years is reasonable. Over three centuries, P inputs from precipitation would have amounted to *ca* 90 kg/ha, and if we assume that net litter P inputs after 70 years equal zero, the P contribution from off-site litter would have been *ca* 20 kg/ha during the first 70 years of forest development.

TABLE 3. *Litterfall P concentration (μg/g), weight (g/yr), and estimated P accumulation (kg/ha/yr) in a primary succession chronosequence of landslide scars and one late-succession vegetation association, Luquillo Experimental Forest, Puerto Rico.*

Age class (years)	Litter weight (g/yr)	P concentration (μg/g)	P accumulation (kg/ha/yr)
1986–1991	34.8	433	0.58
1972–1979	26.8	513	0.65
1951–1964	76.1	257	0.76
CDF* (*ca* 300 yr)	185	210	1.59

* *Cyrilla*-dominated forest.

DISCUSSION

Concentrations of labile P fractions in the chronosequence of landslide scars in the LEF are comparable to values for highly weathered soils tabulated by Sharpley *et al.* (1987; $N = 40$) and Cross and Schlesinger (1995; $N = 6$). Both the concentration and quantity data indicate an increase in labile P (resin-Pi + HCO_3–Pi + HCO_3–Po) in the upper 10 cm of soil resulting from accumulating allochthonous litter P and atmospheric P inputs and possibly from the pool of occluded P. Re-

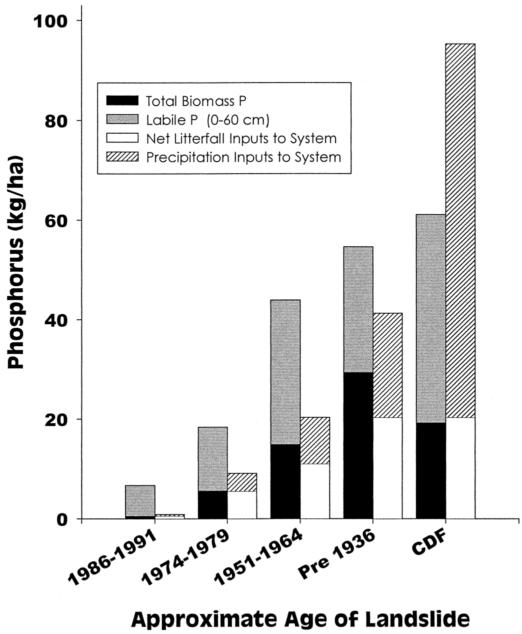

FIGURE 4. Phosphorus stock values (kg/ha) from estimated litterfall inputs, estimated atmospheric inputs, total biomass, and labile P (0–60 cm depth) in the Luquillo Experimental Forest, Puerto Rico. Litterfall values were estimated using values from Table 3. Atmospheric input values were estimated using values from McDowell and Asbury (1994). Biomass (aboveground and forest floor) values were calculated from Zarin (1993). Labile P values were calculated using bulk density values from Zarin (1993) and nutrient concentrations in Table 1.

covering vegetation on the landslide scars apparently assimilates P from those sources and returns it to the soil as organic P in litter where it is further partitioned into several chemical pools. While some mycorrhizae are able to use P from very insoluble pools (Cumming & Weinstein 1990, Read 1991, Paul & Clark 1996), we have no direct evidence that mycorrhizae are using occluded P in LEF landslides, although the other sources of P do not fully account for the total amount of P that accumulates in biomass plus labile P in the soil over 70 years.

Labile P, which we consider to be the pool of P most likely to contribute to plant-available P, was *ca* 6 kg/ha in the youngest landslide scars. This is *ca* 20 percent of the amount of P in live vegetation in the CDF (Zarin & Johnson 1995a; Fig. 4). Immediately after a landslide, the supply of P in primary minerals (dilute HCl–Pi) is *ca* 18 kg/ha to a depth of 60 cm in the weathered regolith, suggesting that other sources of P are necessary to account for the P in forests more than 70 years old.

Annual aboveground P requirement for the mature CDF probably does not exceed 3 kg/ha/yr, and is considerably less for the early phases of forest regeneration. While it is not clear how much of, and on what timescale, labile P measured by this method is available to plants, there appears to be at least some labile soil P available during the early phases of forest regrowth, and in the mature forest plot, there was a very large supply of labile P relative to the annual P requirement.

At age 70 and beyond, forest vegetation and soil have accumulated *ca* 50–70 kg P/ha as P in living biomass and labile forms of P in the soil (Fig. 4). Our ability to estimate the relative importance of P inputs from off-site litter, dry and wet deposition relative to P supplied from the occluded P pool was limited by the mass balance approach we used. Our data support the idea that atmospheric deposition, off-site litter, and the occluded P pool each contributed about one-third of the P that accumulated in 70 years. Quantitatively, the depletion of occluded P in the upper 10 cm of soil was 75 kg/ha, considerably greater than the 20 kg/ha of labile P estimated to have come from the occluded P pool by age 70. Phosphorus-bearing primary minerals depleted after many millennia of weathering prior to colonization by plants appears to have contributed very little to the pool of P that biota can access in the post-landslide forest.

BIOHEOCHEMICAL IMPLICATIONS OF LABILE P.—Figure 3 illustrates the relationship between percent C and resin-Pi and between percent C and the labile P pool. Pearson product–moment correlations show that the very labile resin-Pi was strongly correlated with HCO_3–Po and NaOH–Po. These results concur with the findings of others who have studied acidic, highly weathered soils (Tiessen *et al.* 1984). They are also consistent with the idea that turnover of easily mineralized organic P through microbial mediation is an important control on plant-available inorganic P in LEF forests over 55 years old. Several publications on P in highly weathered tropical soils have indicated that organic matter mineralization is the most important process providing labile P to plants (Adepetu & Corey 1976, Tiessen *et al.* 1994, Selles *et al.* 1997).

The picture that emerged from this chronosequence study is that after a major soil-removing disturbance, there is a net increase in labile P supplied from at least two sources (atmospheric deposition and allochthonous litter input) and probably a third source (the pool of inorganic occluded P). The added P is captured by forest biota and returned to the soil in organic combinations. In the longer term (decades), it appears that the most important source of plant-available P shifts to the labile Po pool whereby vegetation relies on the processing and cycling of readily mineralizable organic P.

Some of the quantitative aspects of P capital recovery are provocative in that they are not predicted by some of the current models of P behavior in highly weathered soils. The net accumulation of labile P in recovering landslide scars is nearly 1 kg/ha/yr. Like cation nutrients Ca, Mg, and K, labile P in the soil appears to be a resilient commodity in this disturbance-prone landscape given the nature and scale of rainfall events, landslides, and Puerto Rico's location in the tradewind belt. Since most slides are small ($\ll$1 ha), a sizable portion of the recovering labile P pool comes from the surrounding forest. Similarly, the high annual rainfall and putative cloud water input provides a significant amount of P to the montane rain forests that grow at this elevation. Even without exogenous inputs, our mass balance data suggest that there are likely internal mechanisms (*e.g.,* mycorrhizae) that allow for release of P bound in the occluded pool.

The annual P required by older forests in the landslide chronosequence for wood and foliage production is less than 3 kg/ha/yr, a figure that is reasonably comparable to the mean value (5 kg/ha/yr) determined for a suite of 20 temperate forests (Johnson & Lindberg 1992) and some other tropical forests (Lugo & Murphy 1986, Tiessen *et al.* 1994, Kitayama *et al.* 2000). In the LEF, after *ca* 30 years, the supply of labile P in the soil as measured by the Hedley fractionation procedure, far exceeds the annual demand for P. It remains to be determined if the labile P fractions measured by this fractionation procedure truly represent P available to plants "in the short term" as suggested by Tiessen and Moir (1993), Tiessen *et al.* (1984, 1994), and Cross and Schlesinger (1995).

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