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Variations in Belowground Carbon Storage and Soil CO_2 Flux Rates along a Wet Tropical Climate Gradient[1]

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ABSTRACT

We used a humid tropical elevation gradient to examine the relationships among climate, edaphic conditions, belowground carbon storage, and soil respiration rates. We also compared open and closed canopy sites to increase the range of microclimate conditions sampled along the gradient, and determine the effects of canopy openings on C and P storage, and C dynamics. Total soil C, the light C fraction, and all of the component fractions of the P pool were significantly related to soil moisture, and all but total soil C were also significantly related to temperature. Both labile and recalcitrant soil P fractions were negatively correlated with the light C fraction, while the dilute HCl-extractable P pool, generally thought of as intermediate in availability, was positively correlated with light C, suggesting that P may play an important role in C cycling within these systems. Total fine root biomass was greatest at 1000 m elevation and lowest at 150 m, and was strongly and positively correlated with soil moisture content. Soil respiration rates were significantly and negatively correlated with fine root biomass and the light C fraction. In forested sites, soil respiration rates were strongly and negatively correlated with total belowground C pools (soils + roots + forest floor). Belowground C pools did not follow the expected increasing trend with decreases in temperature along the gradient. Our results indicated that in humid tropical forests, the relationships among soil C and nutrient pools, soil respiration rates, and climate are complex. We suggest that frequent and prolonged anaerobic events could be important features of these environments that may explain the observed trends.

Key words: *disturbance; phosphorus; Puerto Rico; rainfall; temperature; tropical montane forest.*

The effects of impending climate changes on tropical forest C and nutrient cycling has been a topic of considerable recent interest as scientists and policy makers strive to identify priorities for mitigating the consequences of increasing atmospheric CO_2. Most global circulation models predict that climate in equatorial regions will change much less than in higher latitudes, and the resulting effects on ecosystems will be less severe (Neilson 1993, Ojima *et al.* 1993, Sellers *et al.* 1996). Recent empirical and modeling studies, however, suggest that C storage and fluxes in tropical forests are likely to be highly sensitive to even small changes in climate (Townsend *et al.* 1992, 1995; Vitousek *et al.* 1994; McKane *et al.* 1995; Tian *et al.* 1998). This could have a large impact on global C cycling as tropical forest soils currently store approximately ten percent of the terrestrial soil C pool (Brown & Lugo 1982) and have the highest rates of soil respiration globally (Raich & Schlesinger 1992). Soil respiration rates have been shown to be positively correlated with temperature and precipitation at regional and global scales (Fung *et al.* 1987, Raich & Schlesinger 1992, Raich & Potter 1995). In Hawaiian soils, rates of soil CO_2 flux increased with increasing temperature when precipitation was held relatively constant (Townsend *et al.* 1995). The potential effects of climate change on tropical soil C storage are less well understood (Silver 1998), but are likely to be both direct (Townsend *et al.* 1992), as well as indirect, through effects on nutrient availability and C:nutrient ratios in tissues and soil. The role of P availability is thought to be of particular importance to soil C storage and respiration rates (McKane *et al.* 1995).

Few empirical studies have looked at the effects of climate and edaphic factors on soil C storage and respiration rates in tropical forests. In this study, we used a tropical elevation gradient to explore the relationship of climate to belowground C and nutrient pools and soil CO_2 fluxes. Elevation gradients are convenient systems to study the effects of incremental changes in climate on biogeochemical processes in tropical forests. Considerable research has been conducted along tropical elevation gradients that examined litterfall net primary productivity (Proctor, Anderson, Fogden *et al.* 1983; Proctor, Anderson, & Vallack 1983; Heaney & Proctor 1989; Pendry & Proctor 1996; Raich *et al.* 1997; Silver 1998), decomposition (Anderson *et al.* 1983, Heaney & Proctor 1989, Vitousek *et*

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al. 1994, Silver 1998), and soil nutrient pools (Proctor, Anderson, Fogden *et al.* 1983; Vitousek *et al.* 1988, 1992; Grieve *et al.* 1990; Kitayama 1992; Pendry & Proctor 1996). Elevation itself offers no strong ecological link to ecosystem C dynamics, but often serves as a surrogate for changes in climate by integrating direct and indirect effects of gradients in temperature and precipitation. Carbon storage and fluxes along tropical elevation gradients are likely to be controlled by a complex interaction of climate and edaphic conditions. In a recent review of the literature, Silver (1998) reported that litterfall generally decreased with increasing elevation, but was not directly correlated with temperature and/or rainfall across studies. Similarly, decomposition rates tended to decrease with increasing elevation and were significantly and positively correlated with litter N content, but not with climate parameters.

In this study, we examined the relationships among micro- and macroclimate, belowground C and nutrient pools, and soil respiration rates along an 800-m elevation and climate gradient. We also expanded our ecological gradient by including sites that experienced canopy disturbance. Canopy disturbance can result in short- or long-term changes in C storage and soil CO_2 evolution due to increased temperatures and moisture, labile C sources, and nutrient availability (Stuedler *et al.* 1991, Townsend *et al.* 1995, Laurance *et al.* 1998). We compared sites in which the original canopy cover had been gone for at least five years to sites under intact forest canopies at each elevation.

STUDY SITE AND EXPERIMENTAL DESIGN

The study was conducted along an 800-m elevation gradient in the Luquillo Experimental Forest (LEF) Puerto Rico (18°18′N, 65°50′W) encompassing subtropical wet, subtropical lower montane wet, and subtropical lower montane rain forest life zones (*sensu* Holdridge *et al.* 1971; Table 1). All sites in this study were located on ridges or upper slopes. At each site, forested and open canopy sites were sampled. Open sites consisted of areas in which forested canopy had not recovered for at least five years following disturbance.

Our elevation gradient corresponded to a macroclimate gradient. Mean annual precipitation increases from 2900 mm/yr at the low elevation sites up to just under 5000 mm/yr at the top of the gradient (Brown *et al.* 1983). Mean annual temperature decreases from 24.6 to 20.7°C with in-

TABLE 1. *Edaphic and vegetation characteristics of the study sites along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico.*

Study site and dominant species	Life zone	Species richness (Number/ha)	Cause of opening	Open vegetation	Elevation (m)	Soil type
Short cloud forest *Tabebuia rigida*	Subtropical lower montane rain forest	15	Storm event	Herbaceous species	1000	Clayey Ultisols
Upper colorado forest *Cyrilla racemiflora*	Subtropical lower montane wet forest	40	Storm event	Herbaceous species	780	Clay-loam Ultisols
Lower colorado forest *Cyrilla racemiflora*	Subtropical lower montane wet forest	40	Treefall	Herbaceous species	660	Clayey Ultisols
Tabanuco forest *Dacryodes excelsa*	Subtropical wet forest	50	Experimental canopy opening	Early successional trees, herbs, and tree ferns	290	Clayey Ultisols
Remnant lowland wet forest *Dacryodes excelsa*	Subtropical wet forest	50	Conversion of land use to pasture	Pasture grass	180	Clayey Ultisols

creasing elevation (Garcia, pers. comm.). The climate is aseasonal, with no month receiving <200 mm of precipitation (Scatena 1989).

The underlying parent material for all sites is volcanoclastic sandstone, rich in ferromagnesium minerals of early Cretaceous and early Tertiary age (Bonnet 1939, Beinroth 1982, Scatena 1989). Soils are highly weathered Ultisols, characterized by high clay and Al and Fe content.

MATERIALS AND METHODS

Sampling and analysis of soil CO_2 flux.—We measured soil CO_2 flux rates during seven evenly spaced sampling periods at each site over five weeks in June and July 1997. All sampling was done between 0900 and 1600 h, and the seven sampling periods were distributed throughout the day at each site. This was done to incorporate some of the natural diurnal heterogeneity in soil processes. Sampling was conducted under conditions of light rain, mist, and full sun as they occurred throughout the sampling period. To avoid potentially confounding effects of chamber installation, soil CO_2 flux was measured at a new location for each sampling date, but all samples at a given site were taken within an area of 10 × 10 m. Soil CO_2 flux was measured using the dynamic chamber technique (Hutchinson & Mosier 1981) and a LI-COR 6400 infrared gas analyzer (IRGA; LI-COR, Lincoln, Nebraska). This instrument measured both H_2O and CO_2, and automatically corrected for atmospheric water vapor. Three 25-cm diameter rings were set into the ground to a depth of *ca* 2 cm at each site, 30 min before measurements were taken, to minimize any effects of chamber installation (Keller, pers. comm.). For each measurement, a molded PVC cover was placed on the ring and the gas analyzer attached. Carbon dioxide concentrations in the chamber were measured every 15 sec for 5 min. We took three sets of concentration readings for each ring, yielding a total of nine sets for each site on each sampling date. Soil CO_2 flux was calculated by multiplying the slope of CO_2 concentration in the chamber against time, correcting for chamber volume, chamber temperature, and pressure. The CO_2 flux rates measured here were not annual flux rates, but rather short-term estimates, which were used to explore relationships among soil CO_2 evolution, microclimate, and edaphic factors along the gradient.

Microclimate measurements.—We measured soil and air temperature and soil moisture simultaneously with soil respiration. Soil and air temperatures were measured during each sampling period as the mean of the three samples per site and date, reported as the mean of samples taken at 2- and 10-cm depths using a YSI Tele-Thermometer (Yellow Springs Instrument Company, Yellow Springs, Ohio). Air temperature was measured using a shaded Fisherbrand thermometer at 1 m above the soil surface. Five soil cores to a depth of 10 cm were collected per site using a 2.5-cm corer. The cores were well mixed, and a 5-g subsample was dried at 105°C for 48 h to determine gravimetric soil water content.

We also compared root biomass and soil C, N, and P pools with our microclimate measurements. While it is likely that soil C and nutrient pools and root biomass respond to climate over a longer time period, evidence suggested that short-term, relatively small scale changes in temperature or moisture can have a significant effect on root biomass, and other plant and soil biotic activity (Silver & Vogt 1993, Tian *et al.* 1998). Our comparisons serve as estimates of the relative changes along the gradient, and are likely to be representative of the longer-term trends due to the aseasonality of the ecosystems along the gradient.

Root biomass.—Roots were sampled with a 6-cm diameter root corer using standard techniques (Vogt & Persson 1991). Three cores were taken from random locations within each site. Samples were taken from the 0–10 cm soil depth, in which the majority of the fine roots were concentrated (Silver & Vogt 1993). Roots were stored at 4°C for up to six weeks, at which time they were processed. Roots were washed through a series of three Nalgene sieves (sieve opening sizes: 2.0, 0.5, and 0.2 mm, respectively) to remove soil particles, and were sorted by size class (≤2, >2 to ≤5, and >5 mm diam.); the smallest size class was further sorted into live and dead categories. Only roots in this size class are reported here. All roots were dried at 65°C and weighed to determine mass.

Forest floor mass and nutrient cations.—Eight quantitative samples of forest floor were collected from random locations at each site using a wooden template with internal dimensions of 15 × 15 cm. Forest floor was composed of recently fallen litter and partially humified organic material. Samples were oven-dried at 65°C to determine mass and finely ground in a Wiley mill. Subsamples (three per cover type and site) were analyzed for total C and N on a CE Instruments NC2500 soil analyzer

at the University of California–Berkeley (UC–Berkeley). Forest floor nutrients were analyzed following digestion in HNO_3 (Luh Huang & Schulte 1985) on a DCP Spectrascan V spectrophotometer at the IITF/USDA Forest Service laboratory in Rio Piedras, Puerto Rico, for total Al, Ca, Fe, K, Mg, Mn, and P.

Bulk density and soil elemental conconcentations.—We dug one 15- × 15- × 10-cm quantitative pit at each site for soil chemical and physical analyses. The pit was excavated by 0–2 and 2–10 cm depths. Total soil weight minus rocks and large roots was measured and a subsample dried at 105°C for air- to oven-dry conversions. The results from our bulk density analysis were within the range of values previously found for these ecosystems (Silver *et al.* 1999, Olander *et al.* 1998). Previous work in these systems has suggested that bulk density was not highly variable across short (tens of meters) distances.

Additional subsamples were digested in H_2SO_4–$LiSO_4$, following a predigest in H_2O_2 (Parkinson & Allen 1975). Digest solutions were analyzed for total Al, Fe, and P on a DCP Spectrascan V spectrophotometer at IITF. Soils from the quantitative pits were ground and duplicate subsamples were analyzed on a CE Instruments NC2500 soil analyzer for total C and N at UC–Berkeley. An additional set of samples was taken using a 2.5-cm soil corer. Five to six cores were taken to a depth of 10 cm at each site and homogenized. Samples were analyzed for total C, N, P, Al, and Fe as above.

Soil C fractions were analyzed using the techniques in Trumbore (1984). Soil from each site was separated first by a density fractionation using sodium polytungstate (density 2.2 g/cc, Geoliquids Inc., Prospect Heights, Illinois). The heavy fraction from the density fractionation was separated further into acid (6 N HCl) hydrolyzable and non-hydrolyzable fractions. Organic matter content of the light fractions and heavy acid non-hydrolyzable fractions were determined by ashing at 550°C in a muffle furnace for 5 h. Carbon content for each fraction then was calculated as 45 percent of the organic matter content. Soil C fraction analysis was done on soils from both cores and pits.

Soil P fractions were determined on soils from the quantitative pits using the modified Hedley sequential extraction technique described in Tiessen and Moir (1993). For each sample, sequential extraction separated the total P into six fractions defined by the extractant: anion exchange resin, $NaHCO_3$, NaOH, 1 M HCl (dilute HCl), concentrated HCl, and residual. Extraction solutions were analyzed on a Thermo Jarrell Ash IRIS ICP at UC–Berkeley.

TABLE 2. *Mean values for soil CO_2 flux measurements at sites along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico. Standard errors are given in parentheses,* N = *7 for all sites. Uppercase letters identify significant differences at the 95 percent level within cover type and across elevations. An asterisk identifies significant differences at the 95 percent level between cover types within elevation groups.*

	Soil CO_2 flux μmol $CO_2/m^2/sec$	
Elevation (m)	Forest	Open
1000	2.24 (0.39)[a]	1.60 (0.16)[a]
780	13.48 (2.25)[b]	9.65 (2.14)[b]
660	4.97 (1.02)[a]	4.27 (0.59)[a]
290	10.80 (0.79)[b]	8.98 (0.69)[b]
180	10.05 (1.23)[a]	4.46 (0.34)[a]

Statistical analysis.—Statistical analyses were performed using Systat 7.0 (Wilkinson 1997). Data were log transformed when appropriate to meet the assumptions of analysis of variance (ANOVA). For soil CO_2 flux, analyses were done on the means of each sampling day. Residuals of all analyses were checked for normality and homogeneity of variance (Steel & Torrie 1980). We used ANOVA to determine if variables differed among sites. Paired comparisons using the least significant difference protocol were performed to determine where significant differences occurred. Simple linear and stepwise multiple linear regressions were performed to determine if elevation, microclimate, root biomass, and/or soil physical and chemical characteristics could be used to predict rate of soil CO_2 flux. Each of the measured soil characteristics was compared to each other, elevation, and microclimate using a Pearson's correlation analysis. Significance was determined as $P \leq 0.05$ unless otherwise noted.

RESULTS

CO_2 flux rates and microclimate.—Soil CO_2 flux rates varied significantly among sites (Table 2). Mean CO_2 flux rates were higher under forest canopies compared to adjacent open sites, but this difference was only statistically significant at the lowest site (Table 2). In forested sites, mean soil respiration rates were negatively correlated with the

TABLE 3. *Mean values for microclimate measurements at all sites along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico.* N = *7 for all measurements. Standard errors are given in parentheses. Uppercase letters identify significant differences at the 95 percent level within cover types and across elevations. Asterisks identify significant differences at the 95 percent level between cover types and within elevation groups.*

Elevation (m)	Soil temperature (°C)		Soil moisture (%)		Air temperature (°C)	
	Forest	Open	Forest	Open	Forest	Open
1000	21.3 (0.01)^{A}	22.6 (0.3)^{A*}	65 (2)^{A}	57 (2)^{A*}	25.0 (0.1)^{A}	25.0 (0.2)^{A}
780	22.3 (0.1)^{B}	24.1 (0.5)^{B*}	44 (1)^{B}	53 (1)^{B*}	26.1 (0.2)^{A}	27.3 (0.4)^{A*}
660	23.1 (0.2)^{C}	24.2 (0.4)^{C*}	45 (1)^{B}	51 (2)^{B*}	27.7 (0.3)^{B}	27.7 (0.3)^{B}
290	25.7 (0.1)^{D}	27.1 (0.1)^{D*}	43 (1)^{B}	51 (1)^{B*}	30.7 (0.4)^{C}	32.0 (0.3)^{C}
180	26.7 (0.2)^{E}	31.4 (0.9)^{E*}	31 (1)^{C}	34 (1)^{C*}	33.9 (0.6)^{D}	35.1 (0.8)^{D}

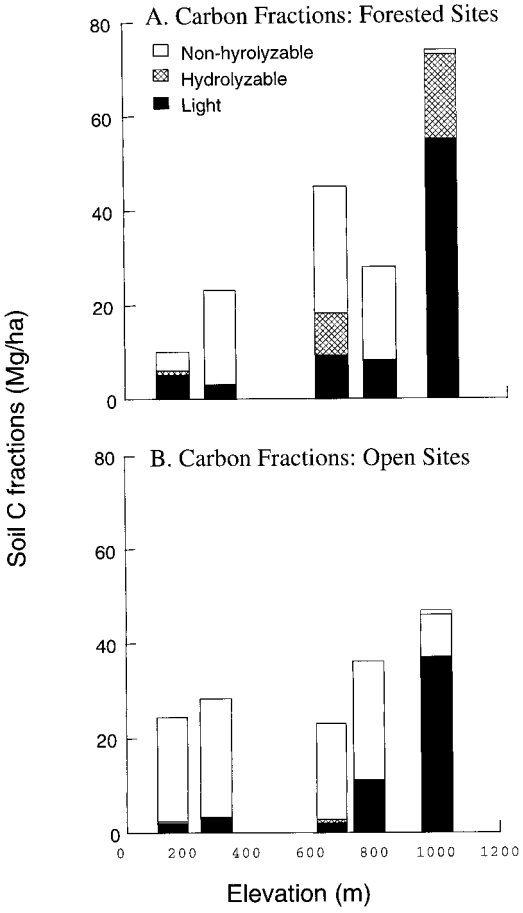

FIGURE 1. Soil C fractions from the 0–10 cm depth along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico. The solid represents the light fraction (density <2 g/cm^3), the crosshatch represents the portion of the heavy fraction that is hydrolyzable in HCl, and the horizontal lines represent the portion of the heavy fraction that is not hydrolyzable in HCl. Fractions are reported in units of Mg/ha. Values for forest sites are shown in 1A and open sites in 1B.

total belowground C pool (roots + soil + forest floor; $R^2 = 0.86$, $P < 0.05$). In the open sites, this relationship was not significant. There were no significant trends in soil respiration with elevation, even though microclimate changed predictably along the gradient (Table 3). Both soil and air temperatures were significantly and negatively correlated with elevation ($R^2 = 0.87$, $P < 0.01$ and $R^2 = 0.97$, $P < 0.001$, respectively). In contrast, soil moisture had a positive relationship with elevation ($R^2 = 0.58$, $P < 0.01$). Elevation trends in soil moisture and soil temperature were similar in forested and open sites along the gradient; however, forested sites had significantly lower values for both variables when compared to open sites at the same elevation, with the exception of soil moisture at 1000 m elevation. Air temperature was similar in forested and open sites (Table 3).

Carbon and nitrogen pools.—Sites in this study varied dramatically in the amount of soil C and the proportion of the various C fractions (Fig. 1). The sites at 1000 m elevation stored the most soil C with 74 Mg/ha C in the forest soils and 47 Mg/ha in the open sites. In contrast, the soils of the tabanuco forest at 290 m elevation stored only 21 Mg/ha under forest and 27 Mg/ha in the open site. It was also clear that cover type had an impact on the amount of C stored in the soil, but the effect was not consistent across all sites (Fig. 1). While variation in total soil C pools among the sites was dramatic, it showed only a weak positive relationship with elevation and soil moisture (Table 3). Total soil C was also positively related to total soil N ($R^2 = 0.46$, $P < 0.05$). Nitrogen followed no trends with elevation or microclimate.

Fractionation of the total soil C pool into light (density ≤2 g/cm^3), heavy, hydrolyzable (density >2 g/cm^3, hydrolyzable in concentrated HCl), and heavy, non-hydrolyzable (density >2 g/cm^3, not

TABLE 4. *The relationship of soil respiration to soil edaphic conditions of samples collected along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico. The* R^2, P *values, and correlation coefficient (r) are simple linear regressions.*

	Soil CO_2 flux		
	R^2	P	r
Total fine root biomass	0.37	0.06	−0.61
Dead root biomass	0.36	0.07	−0.60
Light C fraction	0.35	0.07	−0.59

hydrolyzable in concentrated HCl) pools allowed for a more detailed analysis. The study sites showed big differences in the proportions of the three fractions (Fig. 1). At 1000 m elevation, 69 percent of the total pool was light fraction C, averaging 55 Mg/ha, while the open site at 150 m had only 2 Mg/ha light C, or 10 percent of the total soil C pool. The light fraction was positively correlated with elevation, soil temperature, and soil moisture (Table 4). Soil respiration rates were weakly and negatively correlated with the light C fraction (Table 5), due primarily to the effect of the high light C content and low soil respiration rates at 1000 m elevation.

Root biomass and forest floor measurements.— Total fine root biomass in the top 10 cm of soil ranged from 1.0 (±0.5) to 5.6 (±0.8) Mg/ha along the gradient (Table 6). There were no significant differences in total fine root biomass between for-

TABLE 5. *The relationship of soil respiration to soil edaphic conditions of samples collected along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico. The* P *values and correlation coefficient (r) are simple linear regressions. Cover types are combined for single variable comparisons: the total belowground C pool relationships are for forested sites only.*

	Soil CO_2 flux	
	P	r
Total fine root biomass	0.06	−0.61
Dead root biomass	0.07	−0.60
Light C fraction	0.07	−0.59
Soil C + Forest floor C*	0.02	−0.19
Soil C + Root C*	0.03	−0.20
Forest floor C + Root C*	0.02	−0.18
Soil C + Forest floor C + Root C*	0.02	−0.19

* For forested sites only. Root C was calculated assuming a conversion factor of 0.45 for root biomass.

TABLE 6. *Mean values for total fine root mass (<2 mm diam.), forest floor mass, and forest floor nutrient content at sites along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico. For forest floor mass* N = 8; *for all other values,* N = 3. *Standard errors are reported in parentheses. Uppercase letters identify significant differences at the 95 percent level within cover types and across elevations. Asterisks identify significant differences at the 95 percent level between cover types and within elevation groups.*

Elevation (m)	Fine root mass (Mg/ha)		Forest floor mass (Mg/ha)		Forest floor C (Mg/ha)		Forest floor N (kg/ha)		Forest floor P (kg/ha)	
	Forest	Open	Forest	Open	Forest	Open	Forest	Open	Forest	Open
1000	5.6 (0.8)^{A}	3.9 (0.3)^{A}	20.7 (4.8)^{A}	28.5 (6.6)^{A}	9.4 (2.2)	16.3 (6.7)	224.0 (58.9)	309.4 (154.1)	11.4 (4.7)	13.7 (5.9)
780	2.3 (0.9)^{AB}	1.6 (0.4)^{AB}	11.6 (1.5)^{A}	17.1 (4.3)^{AB}	4.3 (1.6)	11.0 (4.7)	140.3 (44.9)	338.0 (155.6)	4.2 (1.0)	16.4 (6.9)
660	2.9 (0.8)^{AB}	3.4 (1.2)^{AB}	10.9 (3.6)^{A}	10.1 (2.0)^{B}	8.5 (4.2)	4.2 (1.2)	159.1 (6.9)	187.8 (64.7)	6.9 (2.4)	3.0 (0.9)
290	3.0 (1.0)^{AB}	1.0 (0.5)^{AB}	18.2 (2.2)^{A}	8.9 (1.6)^{B*}	7.4 (2.6)	3.0 (1.2)	271.8 (104.1)	106.9 (44.9)	7.0 (2.2)	3.0 (1.4)
180	1.5 (0.3)^{B}	1.5 (0.3)^{B}	17.8 (1.4)^{A}	6.7 (1.3)^{B*}	8.1 (1.3)	3.3 (1.3)	256.8 (70.8)	78.6 (27.8)	5.8 (1.3)	1.4 (0.6)

ested and adjacent open sites. When the two cover types were pooled within elevations, a negative correlation with soil CO_2 flux rates was found (Table 5). Fine root biomass was positively correlated to elevation and soil moisture, and also negatively correlated with soil temperature (Table 4); positive correlations also were found with total soil C content ($R^2 = 0.48$, $P < 0.05$), and the light C fraction ($R^2 = 0.67$, $P < 0.05$). Dead root biomass comprised the majority of the fine root standing stocks, and followed the same trends with soil moisture, temperature, elevation, and soil C pools. The pool of live fine roots was highly variable, ranging from 0 to 19 (±2) kg/ha. Unlike dead roots, live fine root biomass was weakly and negatively correlated with elevation and soil moisture, and more strongly and positively correlated with soil temperature (Table 4).

Forested and open sites exhibited different patterns of forest floor mass (Table 6). In the open sites, forest floor mass showed a strong positive correlation with elevation ($R^2 = 0.80$, $P < 0.05$). Forest floor mass was significantly lower in the colorado forest types (660 and 780 m elev.) than at the other forested sites. Forest floor C content was positively correlated with the light fraction of the soil C pool ($R^2 = 0.59$, $P < 0.01$). Forest floor nutrients varied widely along the gradient (Table 6), but there were no statistically significant trends in forest floor nutrient pools with elevation, soil respiration rates, root biomass, or soil C pools.

PHOSPHORUS FRACTIONS.—The total soil P content showed a significant negative correlation with elevation and soil moisture, and a positive correlation with soil temperature (Table 4). Total soil P was also positively correlated with soil Fe concentrations ($R^2 = 0.77$, $P < 0.01$) and less strongly with Al concentrations ($R^2 = 0.42$, $P < 0.05$).

Most of the different P fractions changed significantly along the elevation gradient (Fig. 2), and also showed distinct relationships with microclimate (Table 4). There was no detectable resin-extractable P in the samples we analyzed with a detection limit of 0.2 (g/g. The relatively labile NaOH-extractable pool and the recalcitrant, concentrated HCl extractable pool were both negatively correlated with elevation and soil moisture, and positively correlated with soil temperature. These pools were also both negatively correlated with the light C fraction ($R^2 = 0.64$, $P < 0.05$ and $R^2 = 0.65$, $P < 0.05$, respectively) and positively correlated with soil Fe concentration ($R^2 = 0.89$, $P < 0.05$ and $R^2 = 0.77$, $P < 0.05$, respectively). In contrast, the dilute HCl-extractable pool, defined as intermediate in availability, was positively correlated with elevation and soil moisture, and negatively correlated with soil temperature (Table 4). The dilute HCl-extractable fraction was also positively correlated with soil C content ($R^2 = 0.55$, $P < 0.05$), light fraction C ($R^2 = 0.56$, $P < 0.05$) and live fine root biomass ($R^2 = 0.40$, $P < 0.01$), and negatively correlated with Fe concentrations ($R^2 = 0.55$, $P < 0.05$).

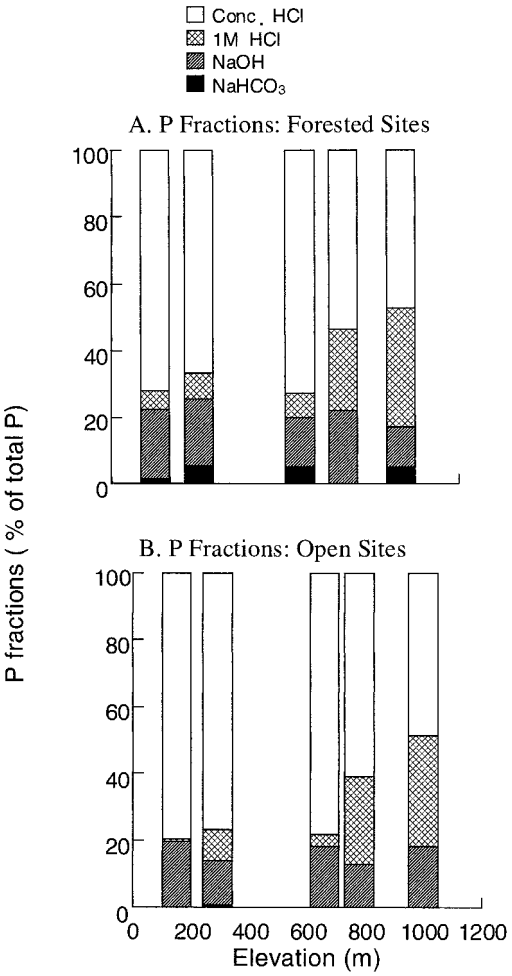

FIGURE 2. Soil P fractions from the 0–10 cm depth, expressed as percentages of the total soil P pool along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico. The solid fill represents the $NaHCO_3$-extractable fraction, the diagonal line fill represents the NaOH-extractable fraction, the horizontal line fill represents the 1 M HCl-extractable fraction, and crosshatch fill represents the concentrated HCl-extractable fraction. Values from forest sites are shown in 2A and open sites in 2B.

TABLE 7. *Mean values for bulk density and total soil elemental content (0–10 cm depth) at sites along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico. Values are from samples that were pooled for analysis. For bulk density,* N = *1; for all other values,* N = *2.*

Elevation (m)	Bulk density (g/cm^3)		N content (Mg/ha)		P content (kg/ha)		Al content (Mg/ha)		Fe content (Mg/ha)	
	Forest	Open	Forest	Open	Forest	Open	Forest	Open	Forest	Open
1000	362	448	3.7	2.4	47.7	36.9	3.5	2.6	1.3	1.5
780	503	539	1.7	1.8	37.4	52.7	3.4	3.1	1.7	1.2
660	461	728	3.7	1.4	81.9	114.6	1.4	4.4	1.5	4.7
290	502	460	1.8	2.6	65.1	81.2	3.0	3.0	2.7	2.5
180	737	802	3.5	1.7	119.3	14.0	5.8	8.2	5.8	6.6

Bulk density and total soil cations.—There were no significant differences in bulk density at the 0–2 and 2–10 cm depths, so all soil analyses are reported on a 0- to10-cm depth basis. Bulk density values showed no significant trend with elevation (Table 7), but values were generally lower under forest than under open cover. Bulk density was negatively correlated with both soil moisture ($R^2 = 0.61$, $P < 0.01$) and fine root biomass ($R^2 = 0.32$, $P < 0.10$), and positively correlated with total soil P content ($R^2 = 0.38$, $P < 0.05$). Aluminum and Fe concentrations were positively correlated with one another ($R^2 = 0.80$, $P < 0.001$).

DISCUSSION

Several of our results contradicted the predictions of current models of C cycling and storage in forest ecosystems. Elevation, soil temperature, and soil moisture were not able to predict rates of soil respiration along our humid tropical elevation gradient. The same was true for belowground C pools (soil, roots, and forest floor). Belowground pools were greater at 1000 m elevation than at 180 m, but contrary to our expectations, the increase in belowground C storage was not strongly related to decreasing temperature and increasing precipitation along the elevation gradient. We did find a strong negative relationship between total belowground C pools (soil + roots + forest floor) and soil respiration rates in the forested sites, but not in the sites that had experienced canopy disturbance.

The strong negative relationship found between belowground C and soil CO_2 efflux may seem counterintuitive, but accumulation of C in soils may be the result of low levels of respiration and decomposition in the coldest, wettest sites on our gradient. The significant increase in the light C fraction with elevation and soil moisture supports this hypothesis, suggesting that decomposition rates are slow in the upper elevations. This is further supported by the data on fine root standing stocks. Previous research has suggested that fine roots are responsible for 30 to 70 percent of the soil CO_2 flux (Schlesinger 1977), and that fine root biomass should be positively correlated with rates of soil respiration. In our study, fine root standing stocks increased significantly with soil moisture, and were positively correlated with total soil C content but negatively correlated with soil respiration rates. This may have been due to slower root turnover in saturated soils, which can augment soil C accumulation and lower root respiration rates.

We hypothesize that the high levels of precipitation and corresponding soil moisture contents in the LEF and typical of tropical rain forests may be responsible for this pattern. Here, the major effect of precipitation may be saturation of soil and creation of anaerobic microsites (Silver *et al.* 1999). Previous work at four of the sites along this gradient has shown that the soils are periodically dominated by anaerobic processes, enough to produce significant levels of methane (Silver *et al.* 1999). Anaerobic conditions are likely to lead to lower soil CO_2 flux rates as microbial populations switch to anaerobic modes of respiration such as methanogenesis. Anaerobiosis also can lead to the accumulation of soil organic matter due to low decomposition efficiency of anaerobic decomposers (Day & Megonigal 1993).

Our analyses of soil P pools also presented some unexpected results, particularly with regard to element interactions. In highly weathered tropical soils, Fe and Al oxides and hydroxides can lead to low P availability (Vitousek & Howarth 1991). Phosphorus is the element most commonly thought of as limiting to plant growth in highly weathered tropical soils (Vitousek & Sanford 1986). Phosphorus fractionation techniques are becoming increasing popular in ecosystem-level stud-

ies, but the ecological relevance of the extractable P fractions has been an area of open debate (Tiessen & Moir 1993, Cross & Schlesinger 1995, Cade-Menun & Lavkulich 1997, Bowman *et al.* 1998). Few studies have related the different fractions to microclimate, soil physical properties, or soil C dynamics in tropical forests.

We found strong positive correlations with both labile and recalcitrant P pools and total soil Fe concentrations. This is likely to be caused by a combination of periodic anaerobiosis in soils along the gradient, which can lead to Fe reduction and release of PO_4 into a NaOH-extractable form (Silver *et al.* 1999), as well as some occlusion of P with Fe in oxidized soils measured in the concentrated HCl and total P assays.

Our findings suggest that the dilute HCl–P fraction could have the most biological significance in this system. This pool was significantly and positively correlated with elevation, soil moisture, total soil C content, and the live root and total root biomass. Calcium phosphates (as measured with the dilute HCl assay) were not expected to be a significant source of P in this system due to the high soil acidity; however, these soils had relatively high Ca concentrations (Silver *et al.* 1994, Olander *et al.* 1998) and $CaPO_4$ potentially could form in less acidic soil microsites. No resin-extractable P was detected in any of the samples, suggesting that the most labile inorganic P was taken up, occluded, or leached from the soil solution as fast as it was supplied.

All measured P fractions were significantly correlated with the light fraction of the soil C pool, elevation, and indices of microclimate. The significant relationships of soil P fractions with C pools and microclimate suggest that P cycling may be sensitive to the direct and indirect effects of climate change in tropical forests. This is particularly interesting given the relatively narrow range of temperature and moisture along the elevation gradient.

The effects of canopy opening on biogeochemistry along the elevation gradient were less clear. The soils in the open sites were warmer and generally moister than their forested counterparts at the same elevation, with the exception of the highest elevation where the open site was warmer but less moist. Surprisingly, there were no differences between forested and open sites in total soil C or C fractions. This may be an artifact of the low sample size and high variability along the gradient and warrants further investigation.

In summary, several aspects of soil C and P pools, root biomass, and forest floor appear to respond to changes in temperature and moisture along the elevation gradient. From the data presented here, it is impossible to determine if these are direct effects or the result of indirect effects such as changes in plant community composition, plant C allocation patterns, or microbial community composition and function. These questions should best be tested with manipulative studies that use the patterns reported here as an experimental template.

The apparent contradictions in the relationships between soil CO_2 flux rates and soil temperature and moisture content in this study and those found at regional and global scales are likely because of high soil moisture content and temperature along the gradient, and the effects of periodic anoxia in saturated soils. At regional and global scales, low soil moisture is likely to limit microbial activity; in contrast, along our study gradient, moisture is never considered limiting, but rather microbial activity is more likely to be limited by excess moisture leading to anoxic conditions at the wetter end of the gradient. Our results highlight the potential usefulness of incremental tropical elevation gradients as a means to test questions of the effects of climate on ecosystem-level processes.

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