

Metabolism of a tropical rainforest stream

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Abstract. Gradients in photosynthesis (P) and respiration (R) were measured on an unperturbed portion of the Rio Mameyes, a tropical stream in the Luquillo Experimental Forest, northeastern Puerto Rico. Rates of P, which were similar to those of streams in temperate-deciduous forests, were low in the heavily canopied headwaters (<70 g O₂ m⁻² y⁻¹) and were higher (453–634 g O₂ m⁻² y⁻¹) in middle and lower reaches. Periphyton biomass did not show the expected increase as the canopy opened downstream, probably because of increasing herbivory in downstream reaches. Rates of R, which were much higher than in most temperate streams, also were lower in the headwaters (767 g O₂ m⁻² y⁻¹) than in the middle and lower reaches (1550–1660 g O₂ m⁻² y⁻¹). High rates of R and suppressed periphyton abundance caused annual P/R to be <<1 from headwaters to lower reaches. Results for the Rio Mameyes suggest that intense herbivory, which is favored by the presence of large herbivores and consistently high temperatures, may be more typical of tropical than temperate streams. Results also show that the tropical rainforest provides the stream with sufficient amounts of labile organic C to support high rates of respiration over long distances across the basin.

Key words: stream metabolism, Rio Mameyes, Puerto Rico, tropical stream, rainforest river.

Tropical streams and rivers could be expected to differ in their metabolism from streams and rivers at higher latitudes because of their higher mean temperature at a given elevation and their greater uniformity in monthly distribution of temperature and incident irradiance. The nature of any such differences may not be simple. Photosynthesis and respiration are affected differently by temperature because temperature and degree of seasonality may influence canopy cover, organic C supply, and other features of terrestrial ecosystems linked to streams. Herbivory, which could alter the rate and balance of photosynthesis and respiration, also may be influenced by temperature and seasonality (Benke 1993). Consistently high temperatures support-

ing rapid growth of herbivores throughout the year could increase the influence of herbivory on primary production (Benke 1993).

Interlatitudinal comparisons of streams spanning elevational gradients (e.g., as described by the river continuum concept; Vannote et al. 1980) are more informative than those based on single locations. Also, interlatitudinal comparisons are weak unless they extend over an entire year because seasonal cycling is one of the most likely differences between tropical and temperate streams. Studies of tropical stream metabolism covering such spatial gradients and extending for at least 1 y are scarce (Talling and Lemoalle 1998), although a few such studies exist (e.g., Dudgeon 1983).

The purpose of our study was to determine if the Rio Mameyes, northeastern Puerto Rico (Fig. 1), shows a balance between photosynthesis (P) and respiration (R) that differs from expectations based on temperate streams of similar size and canopy cover. Two hypotheses were tested across an elevational gradient: 1) tropical streams, because of their perennial warmth, have higher annual rates of P and R than tem-

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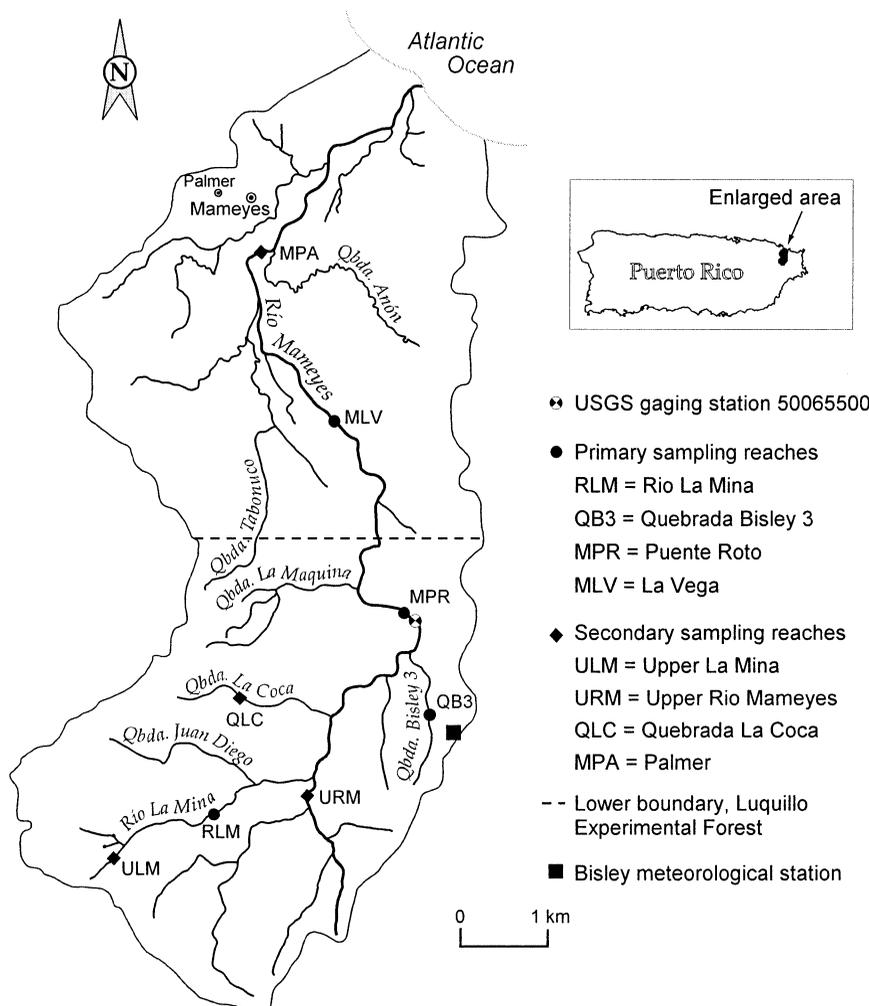


FIG. 1. The Rio Mameyes, Puerto Rico, study site. Qbda. = Quebrada (stream).

perate streams; and 2) P/R ratios for tropical streams are consistently lower than for temperate streams because water temperature affects R more strongly than P.

Metabolism of mountain streams often has been estimated in enclosures (e.g., Bott et al. 1985, Findlay et al. 1997, Naiman and Link 1997, Newbold et al. 1997), although some open-channel estimates exist (Marzolf et al. 1994). Metabolism data based on enclosures may be misleading because enclosures exclude hyporheic R (Naegeli and Uehlinger 1997). We used the open-channel method with improvements developed by Marzolf et al. (1994) that allow its application to mountain streams such as the Rio Mameyes.

Study Site

The Rio Mameyes is 1 of 5 rivers draining the Luquillo Experimental Forest (LEF), a National Science Foundation Long-Term Ecological Research site (Fig. 1). The study reaches extended from the headwaters (~1000 m asl) down to Palmer (80 m asl). No sites were downstream of Palmer, where municipal effluent entered the river. Upstream of Palmer, the basin was in nearly natural condition.

The Rio Mameyes extends 15 km from its headwaters to the Atlantic Ocean and has a basin area of 43 km². The basin is underlain by Cretaceous volcanoclastic rocks and dioritic intrusions (Seiders 1971, Pease and Briggs 1972).

TABLE 1. Physical characteristics of sampling reaches in the Rio Mameyes basin. Reaches are shown in order of decreasing elevation.

	Primary sampling reaches				Secondary sampling reaches			
	Rio La Mina	Bisley	Puente Roto	La Vega	Upper La Mina	La Coca	Upper Mameyes	Palmer
Distance from headwaters (km)	2.0	0.8	6.3	9.0	0.4	1.2	3.4	12.0
Elevation (m asl)	405	250	80	30	670	350	250	10
Reach length (m)	120	50	260	210	75	90	100	150
Mean channel width (m)	7	5	15	17	3	5	12	15
Mean channel slope (%)	8.8	25.6	2.3	0.6	7.7	10.4	5.3	1.4
Mean canopy cover (%)	72	89	39	40	80	88	57	26
Stream order	2	1	3	3	1	1	3	3
Basin area (km ²)	2.8	0.4	17.8	23.7	0.2	0.7	6.0	31.0
% area riffles	70	86	81	38	84	22	60	46
% area pools	20	14	19	62	16	78	40	54
% area runs	10	0	0	0	0	0	0	0
Days since last disturbance (mean)	43	34	47	32	38	37	35	49

Channels in the upper part of the basin are steep, confined, and contain large boulders. In the lower part of the basin, slope of the channel decreases to $\sim 1\%$ (Table 1) and the substrate is predominantly cobble.

Climate in the Rio Mameyes basin is strongly influenced by elevation. Rainfall ranges from 2000 mm/y at low elevations to >4000 mm/y at the highest elevations (Brown et al. 1983). Rainfall occurs in every month, but it is highest in May and from September to November; February, March, and April normally are the driest months (Fig. 2). Mean annual discharge of the

Rio Mameyes prior to the study was $1.6 \text{ m}^3/\text{s}$ (Rio Mameyes at Route 5, USGS 50066000, 3 m asl). Gage records prior to the study showed frequent sharp increases in discharge in response to intense rainfall in the upper basin.

Solar irradiance above the canopy of the Rio Mameyes Basin declines with increasing elevation because of an atmospheric moisture gradient between the coast and higher elevations. The full range of elevation in the Rio Mameyes Basin corresponds to a reduction of $\sim 31\%$ in mean annual irradiance above the canopy between the coast and the headwaters (Bayton 1968, Odum

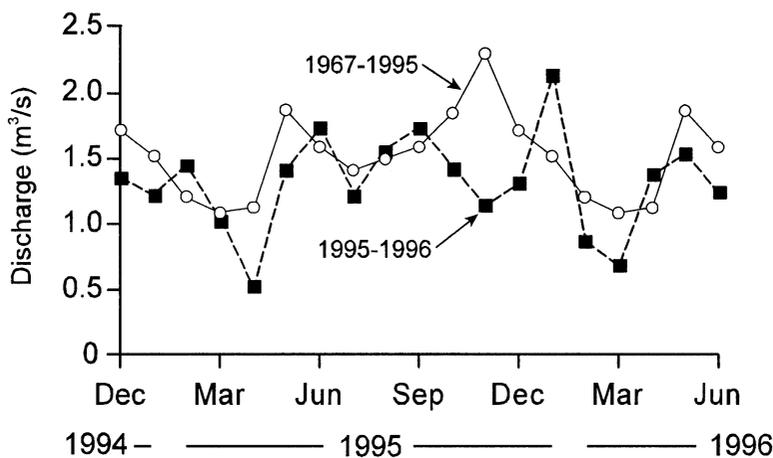


FIG. 2. Mean monthly discharge between 1967 and 1995 and monthly discharge for the study period (1995–1996) on the Rio Mameyes near the Sabana gaging station in the middle of the study area (USGS 50065500, 84 m asl).

et al. 1970). The elevational trend in irradiance could affect the annual rate of stream photosynthesis across the elevational gradient. Mean daily water temperature of the Rio Mameyes ranged from 22°C in February to 24°C in July in the headwaters and from 21°C in February to 28°C in August at low elevation (Ortiz-Zayas 1998).

Methods

Studies of the Rio Mameyes were conducted between February 1995 and April 1996. Rainfall was below average during this period, but variations in discharge allowed sampling over a wide range of flows (Fig. 2). Four primary reaches were sampled every 30 to 45 d, and 4 secondary reaches were sampled less frequently.

Nutrient chemistry

Concentrations of total dissolved P, NO_3^- -N, and NH_4^+ -N were measured at all sites when data on metabolism were collected. All samples were stored in a dark cooler for transport to the laboratory, where they were filtered within 12 h of collection (Whatman GF/F; nominal pore size = 0.7 μm). NH_4^+ -N was determined colorimetrically by a modified Solorzano method (Grasshoff 1976), and NO_3^- -N was measured by ion chromatography. Total dissolved P was determined by a modification of the oxidation method of Lagler and Hendrix (1982) and Valderrama (1981).

Irradiance

Photosynthetically active radiation (PAR) was measured during each diel study as photosynthetic photon flux density (PPFD, $\text{mol m}^{-2} \text{d}^{-1}$) with quantum sensors near the water surface and just over the substrate. Canopy cover was measured with a spherical densimeter placed at randomly selected locations within the sampling reach. In addition, canopy cover was measured at the location of the quantum sensors.

Periphyton

Epilithic periphyton was collected during the diel studies at all sampling reaches. Submerged rocks were selected randomly from 9 equally spaced stream cross-sections within each reach.

Three samples were collected at each cross-section; each sample consisted of 5 rocks. Periphyton samples were taken from each rock by the method of Porter et al. (1993). Subsamples of periphyton biomass were analyzed for both chlorophyll *a* and ash-free dry mass (AFDM). Chlorophyll *a* samples were filtered through GF/C glass-fiber filters, placed in screwcap test tubes, and frozen prior to analysis. Chlorophyll *a* (mg/m^2) was determined by an ethanol-extraction method (Marker et al. 1980), and AFDM (g/m^2) was determined by the gravimetric method of Britton and Greeson (1987).

Disturbances of the bed

Disturbance of the stream substrate, which may affect metabolism, was assumed to coincide with the discharge capable of moving the average streambed particle. Larsen (1997) estimated that the substrate was substantially disturbed at discharges $>22 \text{ m}^3/\text{s}$ at the Sabana gage, although weaker disturbance could have occurred at lower discharges. Time elapsed since the last disturbance (d) was determined for each field sampling date so that the response of periphyton biomass to disturbance could be tested.

Metabolism

P and R were estimated by the open-channel technique of Odum (1956) as modified by Marzolf et al. (1994, 1998) and Young and Huryn (1998); estimates were corrected for the effects of groundwater flux (McCutchan et al. 2002). Field measurements were made of reaeration rate coefficients, diel changes in temperature and O_2 concentration, channel geometry, groundwater flux to the channel, PAR, and periphyton biomass.

The reaeration rate coefficient was measured on 5 dates at each of the primary reaches (Kilpatrick et al. 1989). Propane was injected at a constant rate, and a slug of NaCl was introduced at the upper end of the reach. Travel time was estimated from temporal change in specific conductance associated with transport of the NaCl. Water samples for propane analysis were collected at the top and bottom of each sampling reach with a gas sampler (Kilpatrick et al. 1989). Propane in the headspace of the sample

vials was analyzed by gas chromatography with a flame ionization detector.

Reaeration rate coefficients for O_2 ($k_{\text{oxygen},t}$, /d) were adjusted to standard temperature ($k_{\text{oxygen},20}$) following Kilpatrick et al. (1989). Discharge during reaeration and metabolism studies was estimated from current-meter measurements by the velocity–cross-section method (Gordon et al. 1992).

Reaeration coefficients at primary reaches were not determined concurrently with metabolism studies. Reaeration coefficient at a given reach for any given date can be estimated if a quantitative relationship is developed between discharge and reaeration coefficient. Preliminary screening of various models relating discharge to reaeration coefficient showed that the energy-dissipation model (Tsivoglou and Neal 1976) gave the best results for the Rio Mameyes. This model treats reaeration coefficient as the product of an energy-dissipation value and an escape coefficient, and the energy-dissipation value is defined as the ratio of slope to water velocity (or, equivalently, the ratio of change in elevation to travel time across the reach). The escape coefficient, which incorporates influences on gas exchange not captured by the energy-dissipation value, is determined empirically from measured reaeration coefficients and energy-dissipation values. The relationship between reaeration coefficient, energy-dissipation value, and escape coefficient is quantified as a power function (Tsivoglou and Neal 1976).

The 5 reaeration measurements and accompanying data on slope and velocity for each primary reach were used to calculate escape coefficients, which then were used to develop the power function relating reaeration to energy dissipation and the escape coefficient. The power function then was used to calculate $k_{\text{oxygen},20}$ on dates when metabolism measurements were made at each primary reach.

Reaeration coefficients were not measured at secondary reaches. For geomorphically similar reaches in the same basin, however, the energy-dissipation method allows estimation of $k_{\text{oxygen},20}$ from site-specific energy-dissipation values plus the energy-dissipation power function for geomorphically similar reaches with known escape coefficients (Tsivoglou and Neal 1976). This procedure was used to estimate reaeration coefficients for secondary reaches. A median value for the escape coefficient (0.36/m) from the 3 pri-

mary upper basin reaches (Bisley, Puente Roto, and La Mina; Fig. 1) was used to calculate reaeration coefficients at secondary upper basin reaches (Upper La Mina, Upper Mameyes, and La Coca). The reaeration coefficient for Palmer (primary reach, lower basin) was used for La Vega (secondary reach, lower basin), where geomorphology was similar.

A total of 53 open-channel (diel) estimates of O_2 metabolism were obtained at the 8 sampling reaches. For each estimate, a logging multiprobe sensor (Hydrolab Datasonde III), deployed in situ for 1 to 2 d, measured temperature, dissolved O_2 , and specific conductance at intervals of 15 to 30 min. Elevation and water temperature were used to calculate the O_2 -saturation concentration from the equation of Duke and Marsh (1973). It was assumed that barometric pressure remained constant over the study and that the mean daily sea level pressure was 760 mm Hg. On all dates, the mean daily sea level pressure measured at Roosevelt Roads (20 km east of the LEF boundary) was 760 to 763 mm Hg (National Oceanic and Atmospheric Administration, unpublished data); variation within this range would have affected estimates of the O_2 saturation concentration by $<0.4\%$.

Entry of groundwater within a study reach is not likely to affect estimates of P, but can cause bias in estimates of R if groundwater O_2 deviates significantly from stream O_2 (McCutchan et al. 2002). Rates of groundwater seepage were estimated from paired measurements of discharge and were validated with salt-dilution studies (Ortiz-Zayas 1998). Estimates of seepage for a reach (m^3/d) were divided by the area of the stream bottom to give rates of groundwater flux per unit area of stream bottom (m/d). The O_2 concentration of ground water (4 mg/L) was estimated from data given by McDowell et al. (1992).

For each diel study, net ecosystem metabolism was estimated as follows (McCutchan et al. 2002):

$$P + R = Z(C_t - C_0)/\Delta t - (C_g - C_t)Q_g/A - k_{\text{oxygen}}DZ$$

where P and R are rates of photosynthesis and respiration, respectively ($g O_2 m^{-2} d^{-1}$; R is negative), Z is the mean depth of the channel (m), C_0 and C_t are the initial and final concentrations of O_2 , respectively (g/m^3), C_g is the O_2 concen-

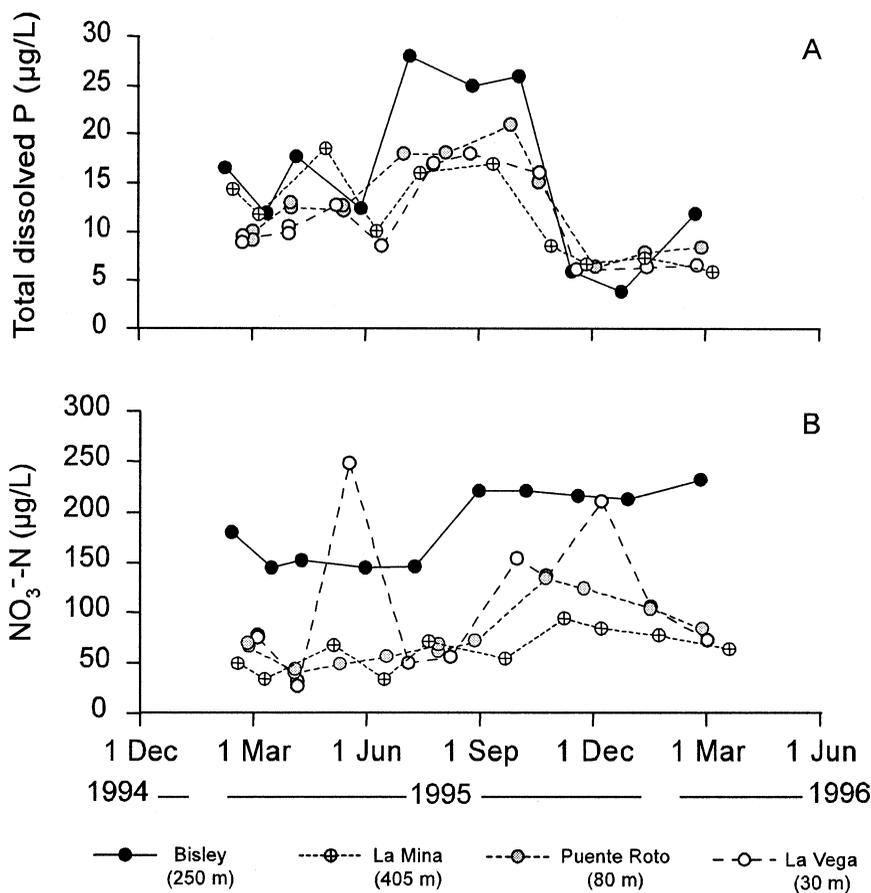


FIG. 3. Concentrations of total dissolved P (A) and NO_3^- -N (B) at the 4 primary sampling reaches. Elevation (m asl) is shown with the name of each station in the legend.

tration of groundwater (g/m^3), Q_g/A is the flux of groundwater per unit area (m/d), k_{oxygen} is the reaeration rate coefficient for O_2 ($/\text{d}$) at temperature T ($^\circ\text{C}$), and D is the saturation deficit for O_2 . Mean depth of each reach was determined from channel-geometry equations for the Rio Mameyes (Ortiz-Zayas 1998). Discharge varied substantially because of rain in the headwaters during some diel studies; thus, data for such dates were not used to calculate metabolic rates. Rates of P and R to be compared across reaches were adjusted to 20°C (P_{20} and R_{20} , respectively) assuming $Q_{10} = 2.0$ (D'Angelo et al. 1997). For P_{20} , rates were adjusted with mean daytime temperature. For R_{20} , rates were adjusted with mean temperature over 24 h. Efficiency of primary production was considered as P/PPFD .

Metabolism was estimated more frequently in

the 4 primary reaches than in the 4 secondary reaches, so data analysis was confined to primary reaches when a statistical trend analysis was based on mean values at a given station. Data from all reaches were used when the data analysis involved trends for individual dates.

Results

Nutrient chemistry

Concentrations of total dissolved P and NO_3^- -N were consistently well above detection limits (Fig. 3A, B). Concentrations of NH_4^+ -N were consistently low (overall mean $\sim 10 \mu\text{g}/\text{L}$) (not shown). The lowest concentrations for total dissolved P tended to occur between November and March, when flows were lowest (Fig. 2, Fig. 3A). Patterns were less well defined for NO_3^- -

N, but minimum NO_3^- -N concentrations also coincided with minimum flow (Fig. 2, Fig. 3B). There were no notable differences in nutrient concentrations among reaches related to distance from headwaters or elevation (Fig. 3A, B). NO_3^- -N concentrations at Bisley were consistently higher than at other stations (Fig. 3B), probably because Bisley was most severely affected by Hurricane Hugo in 1989 (Schaefer et al. 2000).

Irradiance and periphyton biomass

Irradiance reaching the stream surface increased with basin area, except for Upper La Mina, which had an unusually sparse canopy for a stream of its size (Fig. 4A). Irradiance was closely correlated with distance from headwaters ($r = 0.99$). PAR reaching the substrate was nearly identical to PAR at the surface of the water because the streams were shallow and the water was typically clear.

Periphyton biomass (as chlorophyll *a*) did not increase downstream in response to opening of the canopy (Fig. 4B), but variance among sampling dates at each reach was large. AFDM decreased significantly downstream (Fig. 4C). AFDM/chlorophyll *a* ratios were generally high, indicating that AFDM included a large amount of nonautotrophic organic matter. Chlorophyll *a* was correlated closely with AFDM ($r = 0.82$) and with ash ($r = 0.86$). These relationships indicated that periphyton and other particulate matter (organic and inorganic) accumulated simultaneously.

Metabolism

The mean and range of reaeration rate coefficients were directly related to elevation (Table 2). The fit of the power function associated with the energy-dissipation model was good for all reaches except La Vega, which had a nearly constant coefficient across the observed range of discharges; thus, a mean reaeration coefficient was used for all dates at La Vega.

Reaeration rate coefficients for La Mina were much higher than at any of the other primary reaches because of its stair-step channel structure. Plunging flow produced high reaeration rates, as expected, but the uneven distribution of reaeration rates upstream of any given point of measurement undermined the assumption of

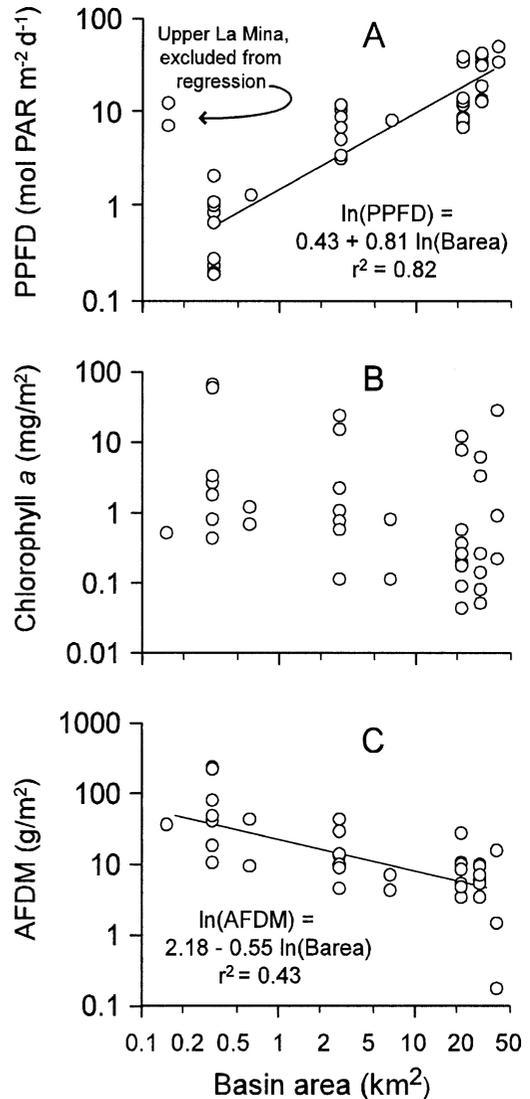


FIG. 4. Relationships of basin area (Barea) to mean photosynthetically active radiation (PAR) at the stream surface (A), periphyton biomass expressed as chlorophyll *a* (B), and ash-free dry mass (AFDM) of biofilm (C). PPFD = photosynthetic photon flux density.

the metabolism calculations that reaeration rate at the measurement point accurately represented mean reaeration rate across the entire reach. For this reason, no calculation of metabolism was made from reaeration rates obtained at La Mina.

Rates of P and R showed no obvious seasonal pattern at the 3 primary reaches where esti-

TABLE 2. Summary of measurements of reaeration rate coefficients at the 4 primary stations ($n = 5$ at each station) and of the application of the energy-dissipation model to each station. Reaches are shown in order of decreasing elevation. – = not statistically significant at $p = 0.05$.

Reach	Type	Reaeration rates (range, /d)	Power function (r^2)	Escape coefficient
Bisley	Upper basin	134–168	0.49	0.360
La Mina	Upper basin	161–691	0.85	0.362
Puente Roto	Upper basin	32–67	0.68	0.120
La Vega	Lower basin	21–27	–	–

mates were possible (Fig. 5A, B). The annual rate of P was low ($69 \text{ g O}_2 \text{ m}^{-2} \text{ y}^{-1}$) at Bisley, at the highest elevation, and was much higher at Puente Roto ($634 \text{ g O}_2 \text{ m}^{-2} \text{ y}^{-1}$) and La Vega ($453 \text{ g O}_2 \text{ m}^{-2} \text{ y}^{-1}$). The annual rate of R at Bisley ($767 \text{ g O}_2 \text{ m}^{-2} \text{ y}^{-1}$) was $\sim 1/2$ the rates of R at Puente Roto ($1550 \text{ g O}_2 \text{ m}^{-2} \text{ y}^{-1}$) and La Vega ($1660 \text{ g O}_2 \text{ m}^{-2} \text{ y}^{-1}$). The annual mean P/PPFD ratio was highest at Bisley and substantially lower at Puente Roto and La Vega (Table 3). P/PPFD ratios varied irregularly over the year at each of the primary reaches (Fig. 5C). P/R ratio was higher at Puente Roto than at Bisley or La Vega (Fig. 5D), but all values were $\ll 1.0$ for the year (Table 3). P_{20} increased with PPFD only up to $\sim 5 \text{ mol m}^{-2} \text{ d}^{-1}$ (15–20% of irradiance over an unshaded stream segment; Fig. 6). All but 2 reaches (Bisley, La Coca) received $>5 \text{ mol m}^{-2} \text{ d}^{-1}$ PAR (Fig. 6).

P_{20} , R_{20} , and the P_{20}/R_{20} ratio increased significantly downstream, as indicated by their positive relationships with basin area (Fig. 7 A, B, C). In contrast, P_{20}/PPFD ratio decreased downstream (Fig. 7D). P_{20} was not correlated with time since the last disturbance, but there was a significant negative relationship between the amount of chlorophyll *a* and time since the last disturbance ($r = -0.48$, $p = 0.0015$) (not shown).

Discussion

Five environmental factors may account for mean P and R and for trends in P and R across stations in the Rio Mameyes: streamwater nutrient concentrations, temperature, irradiance, biomass removal by spates and herbivores, and allochthonous C supply. Streamwater nutrients can be judged by minimum concentrations indicative of limitation, and temperature can be evaluated on the basis of temperature corrections with the assumption of an appropriate Q_{10} .

Degree of accumulation of autotrophic biomass should reflect biomass removal if nutrients are sufficient to support growth. Abundance of labile C supplies can be inferred from R and P/R ratios as a function of distance from headwaters.

Nutrients

Concentrations of total dissolved P and inorganic N in the Rio Mameyes did not reach the extreme degrees of depletion associated with severe growth limitation (e.g., Hall and Tank 2003). Concentrations of NO_3^- -N were similar to those reported by McDowell and Asbury (1994) for nearby basins (discharge-weighted mean = $60\text{--}69 \text{ }\mu\text{g/L}$ NO_3^- -N). In contrast, concentrations of total dissolved P were much higher for the Rio Mameyes than for the rivers studied by McDowell and Asbury (1994), who estimated a discharge-weighted mean of $2 \text{ }\mu\text{g/L}$ for total dissolved P; however, data for soluble reactive P reported by Mulholland et al. (2001) for the Rio Mameyes are consistent with concentrations of total dissolved P reported here (Fig. 3A). Both N and P were available in sufficient amounts to support substantial growth of autotrophs.

Irradiance and biomass removal

Solar irradiance is substantially blocked in the headwaters by canopy and, to a lesser extent, by cloudiness. Solar irradiance is the likely cause of the inverse relationship between P and distance from headwaters in the Rio Mameyes. This pattern is generally expected with the transition from headwaters to intermediate reaches of streams in forested basins (Vannote et al. 1980).

Higher P would be expected to produce higher chlorophyll *a* per unit area downstream, but

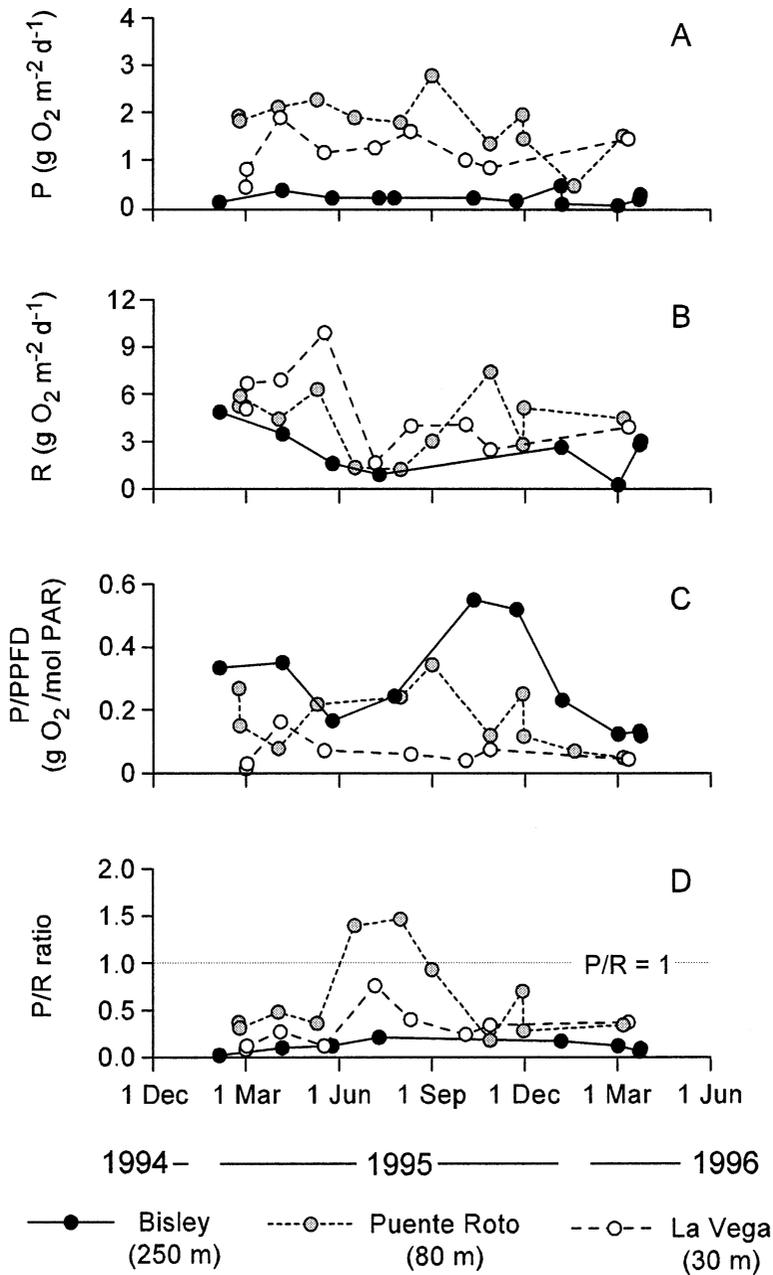


FIG. 5. Seasonal changes in photosynthesis (P) (A), ecosystem respiration (R) (B), P/photosynthetic photon flux density (PPFD) (C), and P/R (D) at the 3 primary sites (elevations asl are shown for each reach). P/R = 1 is shown for reference.

chlorophyll *a* data showed no such increase (Fig. 4B). Thus, removal of biomass is implicated as an explanation for low biomass accumulation in downstream reaches. Spates of sufficient magnitude to move the bed can remove periphyton

biomass (Biggs et al. 1999), but the data do not show a positive relationship between time since disturbance and amount of benthic chlorophyll *a*. Fast recovery of periphyton in the Mameyes (10–14 d; F. Blanco and B. Bryan, University of

TABLE 3. Annual mean (SE) daily rate of photosynthesis (P), P/photosynthetic photon flux density (PPFD), daily rate of ecosystem respiration (R), and P/R ratio measured with the open-channel technique at 3 primary sampling reaches of the Rio Mameyes. PAR = photosynthetically active radiation.

Sampling reach	P		P/PPFD		R		P/R ratio
	g O ₂ m ⁻² d ⁻¹	n	g O ₂ /mol PAR	n	g O ₂ m ⁻² d ⁻¹	n	
Bisley	0.19 (0.03)	12	0.278 (0.157)	11	2.44 (0.52)	8	0.10 (0.03)
Puente Roto	1.77 (0.16)	12	0.173 (0.097)	11	4.07 (0.067)	10	0.39 (0.05)
La Vega	1.15 (0.15)	9	0.061 (0.045)	8	4.96 (0.085)	9	0.30 (0.07)

Puerto Rico, unpublished data) might mask the chlorophyll *a*-disturbance relationship, but a group-comparison test between chlorophyll *a* ≤ 14 d and >14 d after disturbance gave no indication that biomass was strongly controlled by spates. We conclude that spates do not account for suppression of periphyton biomass.

Herbivory also could suppress periphyton biomass accrual in the Rio Mameyes. Large populations of herbivorous shrimp and snails occur in streams of the LEF (Pringle et al. 1993, Pringle and Blake 1994, Covich and McDowell 1996, Pringle 1996, March et al. 2002), and herbivorous fish also contribute to the loss of periphyton (Covich and McDowell 1996). In the Rio Mameyes, herbivores generally increase in abundance and diversity downstream from the headwaters (Covich and McDowell 1996), but it is unknown if intensity of herbivory also increases downstream. Rates of grazing by shrimp probably are highest at high elevations

(March et al. 2002; E. Greathouse, University of Georgia, personal communication), but snails, which are the dominant herbivore by mass in the Rio Mameyes, are most abundant at low elevations ($>500/m^2$ of small snails cf. $20/m^2$ of larger snails at high elevations), suggesting higher herbivory downstream (F. Blanco, unpublished data). March et al. (2002) documented a similar trend in the Espiritu Santo River, which lies within the LEF. A downstream gradient in herbivory could be explained by gradients of habitat suitability and by physical barriers (e.g., cascades) that exclude or reduce the upstream colonizing ability of some herbivores (Covich and McDowell 1996).

Allochthonous C

The exceptionally low P/R ratios of the Rio Mameyes indicate that R is largely disconnected from P because the organic C that supports eco-

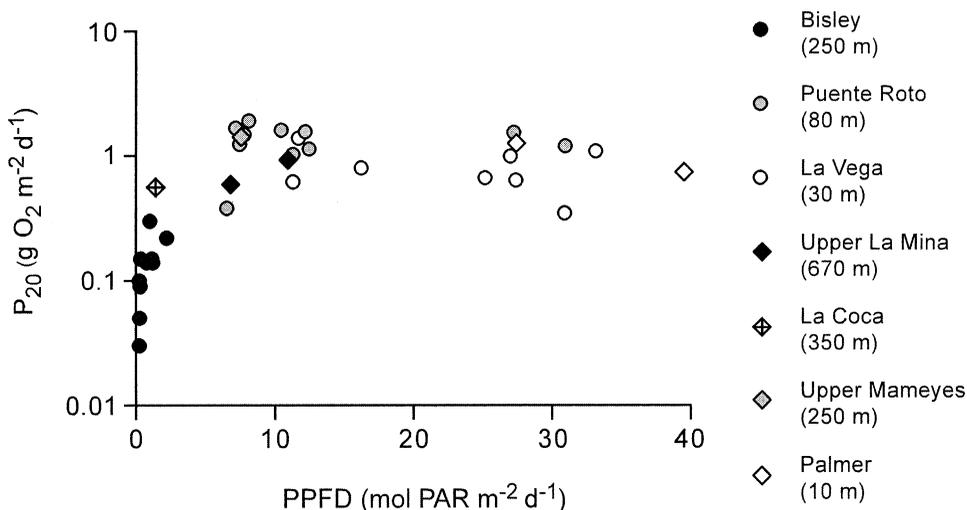


FIG. 6. Relationship between temperature-corrected photosynthesis (P_{20}) and photosynthetic photon flux density (PPFD).

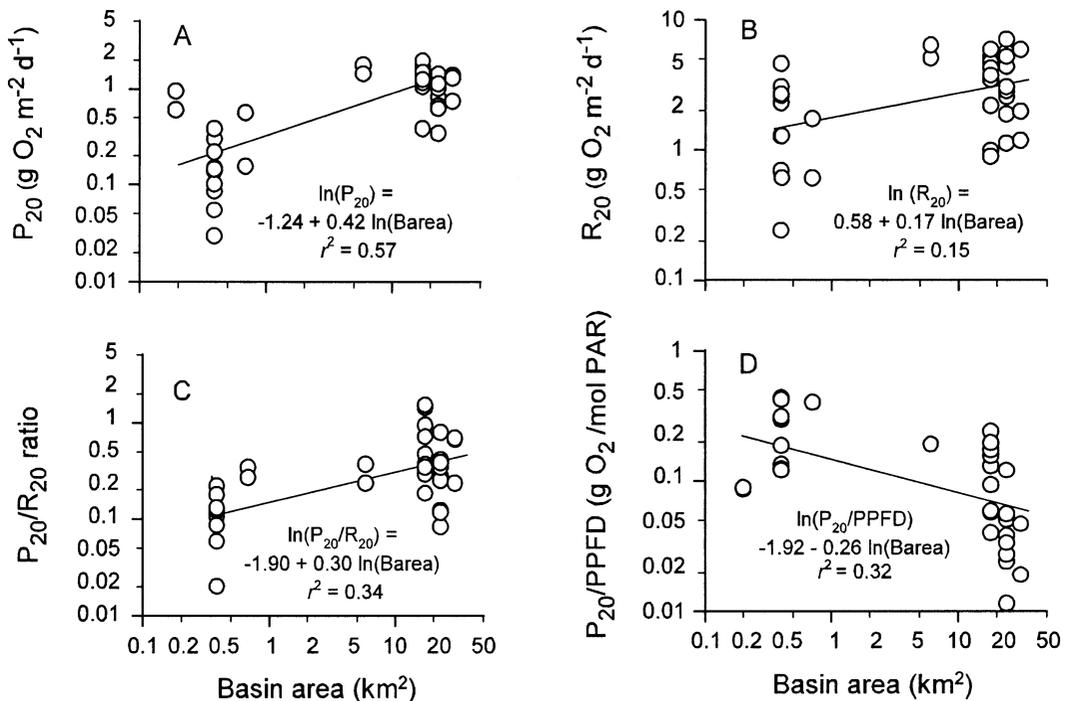


FIG. 7. Relationships between basin area (Barea) and temperature-corrected photosynthesis (P_{20}) (A), temperature-corrected ecosystem respiration (R_{20}) (B), P_{20}/R_{20} (C), and temperature-corrected P_{20} /photosynthetic photon flux density (PPFD) (D) for all sampling reaches. Trend lines are statistically significant ($p < 0.05$).

system R must originate mainly from the basin rather than from autochthonous producers. Measurements of AFDM show that total amount of biofilm decreased rather than increased downstream (Fig. 4C). Therefore, the downstream increase in temperature-corrected R apparently involved increased amounts of labile organic C downstream or increasing transient storage downstream.

Comparison with temperate streams

P generally increases with basin area in streams in deciduous (temperate) forests and streams in coniferous (temperate and boreal) forests, but the rate of increase differs between streams of coniferous and deciduous forests (Webster and Meyer 1997; Fig. 8A). For the Rio Mameyes, the relationship between P and basin area is more similar to that of deciduous forest streams than to that of coniferous forest streams (Fig. 8A). The relationship between R and basin area also differs between coniferous and deciduous forest streams (Webster and Meyer 1997;

Fig. 8B). R in the Rio Mameyes increased with basin area, but was consistently higher than R in deciduous streams of similar basin area. R in the Rio Mameyes was more similar to R in deciduous forest streams than R in coniferous forest streams (Fig. 8B). In the Rio Mameyes, the P/R ratio increased with basin area, as in deciduous and coniferous streams, but estimates of the P/R ratio in the Rio Mameyes were below the trend lines for deciduous or coniferous streams (Webster and Meyer 1997; Fig. 8C).

Our estimates of R are among the highest listed by Sinsabaugh (1997) and are higher than any estimates for temperate streams of comparable basin area, excluding blackwater streams with large floodplains. The Rio Mameyes might be expected to show higher annual R rates than most temperate streams, given the steady and high supply of allochthonous organic matter associated with year-round litterfall (Ortiz-Zayas 1998) and constantly high water temperatures. The Rio Mameyes data are consistent with an empirical relationship between R and mean annual water temperature developed by Sinsa-

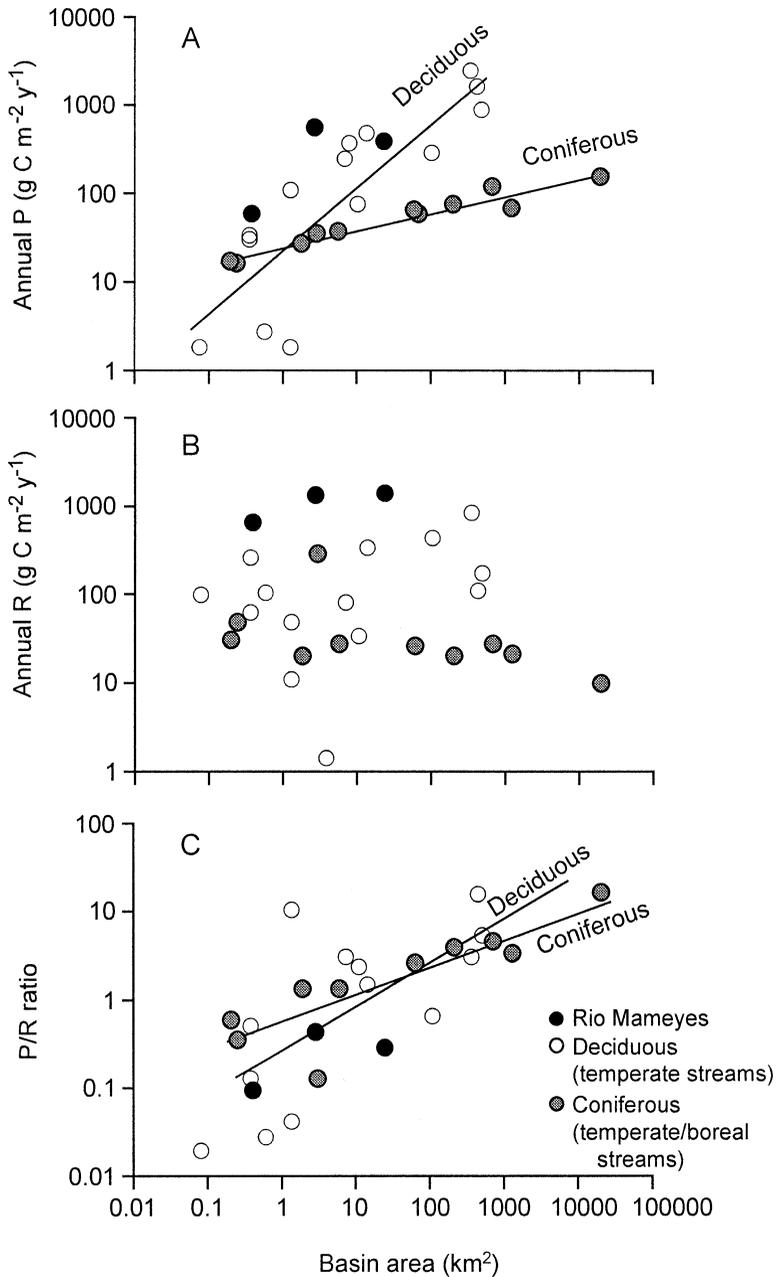


FIG. 8. Annual rates of photosynthesis (P) (A), respiration (R) (B), and P/R (C) for the 3 primary sampling reaches of our study and for sites reviewed by Webster and Meyer (1997). Deciduous = temperate deciduous forest streams, Coniferous = temperate and boreal coniferous forest stream.

baugh (1997) for streams of boreal to subtropical latitudes. Thus, there appears to be a gradient in R across latitude that is explained by temperature acting as a regulator of R, the rate of terrestrial C supply to streams, or both.

Interlatitudinal comparisons of stream metabolic rates suggest differences between temperate and tropical streams. However, such comparisons, especially for R, should be treated with caution because of possible differences be-

tween estimates based on chambers and estimates based on open-channel techniques. Most of the available literature is based on chamber methods (Webster and Meyer 1997, Sinsabaugh 1997), which are likely to underestimate R.

In conclusion, the Rio Mameyes was strongly heterotrophic at all study reaches. This result was unexpected in the downstream reaches where substantial PAR reached the stream bottom. Removal of periphyton biomass by herbivores appears to explain suppression of autotrophic biomass downstream, and low autotrophic biomass probably reduced P in the middle and lower reaches of the Mameyes. High R across all sites was consistent with a latitudinal gradient of R, suggesting that R for tropical streams of specific basin areas is among the highest measured for unaltered streams. Furthermore, high R in the Rio Mameyes throughout the year demonstrates an abundant external supply of labile organic matter in its middle and lower reaches, where autochthonous sources appear weak.

The Rio Mameyes shows the same type of downstream gradients in P that are expected for temperate streams because longitudinal gradients in canopy cover are similar for tropical and temperate forests during the growing season, but herbivory in the Rio Mameyes appears to prevent the biomass accumulation that would be expected at intermediate stream orders (Vannote et al. 1980). It is unclear whether suppression of autotrophic biomass in the Rio Mameyes is linked to its tropical latitude. Year-round high temperature in the tropics allows constant, high growth rates of herbivores (Benke 1993), which may allow herbivory to be more influential than at latitudes where herbivory cycles seasonally (e.g., McCutchan and Lewis 2002). Overall, the Rio Mameyes is surprisingly heterotrophic beyond its headwaters, and the explanation lies in high R coupled with suppressed P caused by low periphyton biomass accumulation.

Acknowledgements

We thank Felix Hernandez, Gustavo Guzman, and Coqui Kent for help with field work. US Forest Service personnel also helped in the field (Carlos Estrada, Don Angel Colon, and Carlos Torres) and with laboratory analyses (Samuel Moya, Andres Garcia, Mary Jean Sanchez, Mirriam Salgado, and Edwin Lopez). US Geological Survey personnel (Pedro Diaz, Heriberto Torres,

Rene Sanchez, and Jose Agis) provided further assistance with this project.

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Received: 1 October 2003

Accepted: 4 August 2005