

## Seasonally variable riverine production in the Venezuelan llanos

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**Abstract.** We examined primary production, respiration, and nutrient dynamics in littoral areas of the mainstem and lagoons of the Cinaruco, a nutrient-poor river in the Venezuelan llanos. Gross primary productivity (GPP) was relatively high, given the poor nutrient conditions in this river. Seasonal variability in net ecosystem production (NEP) was also high, with highest values occurring in the dry season (March–April) when fish biomass and chlorophyll *a* (both water-column and benthic) levels were greatest (dry-season NEP = 542 mg C m<sup>-2</sup> d<sup>-1</sup>, wet-season NEP = 303 mg C m<sup>-2</sup> d<sup>-1</sup>). NEP and algal biomass (measured as chlorophyll *a*) were higher in lagoons than at river sites, with more pronounced differences between these 2 habitats during the dry season. Strong N limitation was evident. Dissolved inorganic N (DIN) concentrations always were <2 μM and typically were <0.5 μM. Molar ratios of DIN:SRP (soluble reactive P) varied little seasonally and were always <8. As in other Neotropical aquatic systems, water-column productivity was an important source of organic matter and was >2× benthic productivity, even in shallow regions of the riverine ecosystem. Low nutrient levels combined with high rates of autochthonous productivity in the littoral zone of this river suggest extremely rapid nutrient cycling rates and support the view that the littoral regions may be important in providing the organic matter that maintains secondary production, consistent with the Riverine Productivity Model and other observations in the Orinoco Basin.

**Key words:** productivity, respiration, nutrients, hydrology, net ecosystem production, N limitation, Venezuela.

The biogeochemistry of tropical rivers is interesting because of the role of these rivers in global cycles and their responses to human impacts such as increased agricultural development, eutrophication, and landscape alteration. Rivers integrate landscape processes because they are tightly connected to the landscape via hydrologic and atmospheric processes. Several con-

ceptual models are relevant to our understanding of foodweb and biogeochemical dynamics in large riverine ecosystems. The river continuum concept (RCC), a model that focuses on longitudinal variation in stream ecosystems, suggests, among other things, that large rivers tend to be net heterotrophic (gross primary production [GPP] < community respiration) in their upper reaches, net autotrophic in their midreaches, and net heterotrophic in their lower reaches (Vannote et al. 1980). Variations in exposure to sunlight and allochthonous inputs are hypothesized to be responsible for these differences. A paradigm more appropriate to

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unimpounded large tropical rivers is the flood pulse concept (FPC; Junk et al. 1989), which emphasizes the role of riparian zone inundation in regulating primary production and foodweb processes. The riverine productivity model (RPM) focuses on the importance of both autochthonous and riparian production, rather than just allochthonous inputs from the floodplain, to in situ production in rivers (Thorp and Delong 1994). Each of these models emphasizes the connections between the landscape and riverine processes, but the 3<sup>rd</sup> model argues that most of the primary production funneled to higher trophic levels in rivers passes predominantly through the autotrophic, rather than the detrital, food chain.

Recent work supports the RPM by demonstrating that rivers can be net heterotrophic (Richey et al. 1990, 2002, Raymond et al. 2000) even when the organic matter that is consumed by higher trophic levels is primarily autochthonous (Thorp and Delong 1994, Lewis et al. 2001, Jepsen and Winemiller 2002, Thorp and Delong 2002). This apparent paradox suggests that much of the allochthonous organic matter transported into rivers is fueling high rates of respiration, mostly microbial (Benner et al. 1995), with little to no effect on upper foodweb dynamics. According to this view, the microbial loop is somewhat disengaged from the rest of the food web, contrary to previous speculation that the microbial loop is an important trophic link, especially in blackwater rivers (Meyer 1990).

Food webs in tropical rivers contain high biodiversity and frequently are dominated by detritus-feeding fishes (Winemiller 1996, Winemiller et al. 2006). Relationships between productivity and diversity have been studied extensively (Tilman 2000, Loreau 2001, Naeem 2002, Herbert et al. 2004), but simple generalizations are elusive, and some of the most diverse ecosystems are those with relatively low nutrient content and biomass levels with high turnover rates and productivity (Herbert et al. 2004). Furthermore, recent work also indicates that diversity of detrital sources can contribute to increased species diversity (Moore et al. 2004).

We examined autochthonous productivity in a species-rich tropical river in the Orinoco Basin. The Cinaruco is characterized by low nutrient concentrations. Previous studies demonstrated that similar rivers in the basin have low algal biomass and productivity (Lewis 1988). Few measurements have been made in this ecosystem, but we hypothesized that littoral areas might be critical to generating and maintaining diversity and productivity (supporting the RPM). However, we did not examine other potentially important energy sources, such as allochthonous organic matter inputs (but see Roelke et al.

2006). We also examined the importance of seasonal hydrological variability for primary production and decomposition processes, which is relevant to the FPC. Last, we took advantage of variation in the abundance of a seasonally migratory benthic-feeding fish (*Semaprochilodus kneri*) to evaluate its potential to exert top-down control on seasonal dynamics at the base of the food web in this river. We hypothesized that increased nutrient regeneration caused by increased consumption of periphyton and detritus by the influx of this and other benthic-feeding fishes in the low-water period might stimulate primary production.

## Methods

### *Study site*

The Cinaruco is a clearwater river with low pH, alkalinity, and conductivity (Montoya et al. 2006). It is located in Venezuela's Santos Luzardo National Park, Estado Apure but, unlike many of the nearby rivers draining the Andes, all of its drainage is from within the llanos. In the llanos, nutrient poor, high quartzite soils underlain by high kaolinite clays (Sarmiento and Pinillos 2001) contribute to high dissolved organic C (DOC) concentrations in surface waters. This allochthonous C is composed of humic and fulvic acids that are colored (Roelke et al. 2006) and absorb visible light. Despite high DOC input, dissolved nutrient levels remain quite low. Productivity in the Cinaruco Basin is further limited by lack of alluvium from the Andean uplands (Sarmiento and Pinillos 2001).

The hydrology of the Cinaruco is strongly seasonal, and this seasonality is also relevant to productivity. The peak low-water period occurs in March to April and the peak high-water period occurs in July to August with transitions (rising-water and falling-water periods) between these low- and high-water periods. Despite relatively low nutrient levels, the river supports  $\geq 280$  fish species (KOW, unpublished data). *Semaprochilodus kneri*, a benthic-feeding detritivore, migrates from the mainstem Orinoco to the Cinaruco during the falling-water period. Therefore, one question addressed in our study was whether some of the changes that occur in the lower food web could be a consequence of top-down (consumer control) effects of this fish (Winemiller et al. 2006).

*Sampling sites.*—We characterized seasonal environmental dynamics in the Cinaruco by sampling physicochemical and production variables in the littoral zones of 5 river sites and 5 lagoon sites in the region of Laguna Larga from January to May 2002 and from November 2002 to July 2003. We were not able to sample the river and lagoons during the peak of the high-water period because of logistical difficulties, but

we were able to make measurements during the falling-water period (November–January), low-water period (March–April), and rising-water period (May–June). All river sites were located on sand bars and were separated by 2 or 3 km. Lagoon sites were located in 4 floodplain lakes that remained connected to the river throughout the study. Two sites were located in Laguna Larga and one each in Laguna Espiñero, Laguna Esse, and Laguna Ojeda. These lagoon sites also had sandy shores of shallow grade (see Montoya et al. 2006 for more details). We took water samples and in situ water-column measurements at each site at a depth of 30 cm below the surface in the littoral zone where the maximum depth was ~1 m.

#### *Metabolic and physicochemical measurements*

*Production.*—We used light and dark benthic chambers (Suplee and Cotner 2002) to measure fluxes of dissolved O<sub>2</sub> (DO) and nutrients (NO<sub>3</sub>, NO<sub>2</sub>, NH<sub>4</sub>, SiO<sub>3</sub>, and soluble reactive P [SRP]) into and out of sediments and to estimate GPP and net ecosystem production (NEP). We did these measurements in March 2002 (dry), May 2002 (rising water), November 2002 (falling water), March 2003 (dry), and May 2003 (rising water) (Montoya et al. 2006). We made all light chamber measurements near midday (from ~1000–1400 h) to minimize variability in solar insolation. We did dark incubations for only ~1.5 h so that DO levels did not decrease significantly from ambient levels. In March and May 2002, we did quadruplicate incubations at each site and made measurements at 6 sites to characterize primary production and ecosystem respiration (R). In other months (November 2002, March 2003, and May 2003), we did one incubation per site at 3 to 5 river sites and 5 to 8 lagoon sites.

We pressed opaque and transparent benthic chambers, each with a propeller to gently mix waters, into the sediments to a depth of ~4 cm. Several of the propellers failed, so we used the propeller associated with O<sub>2</sub> measurements on a Hydrolab H20 internally logging water-quality sonde to mix the chambers. Our visual observations in transparent chambers indicated that turbulence was sufficient to mix the entire chamber (0.1 m<sup>2</sup>; ~8 L). We purged chambers with outside water for 10 min before closing all ports and beginning the incubation. We measured DO concentrations every 5 min with the sonde O<sub>2</sub> probe attached to the top of each chamber and mixed chambers for 2 min prior to measurements. We corrected sediment O<sub>2</sub> demand for water-column O<sub>2</sub> demand using water collected from the site and changes in DO in biological

oxygen demand (BOD) bottles over a 2 to 4 h period (Suplee and Cotner 2002).

We measured water-column GPP and R in 300-mL BOD bottles using the light–dark bottle method (Wetzel and Likens 1991) while the benthic chambers were deployed. We filled bottles with water from the site and incubated them at ~0.7 m depth. We measured changes in DO concentrations (Wetzel and Likens 1991) using a YSI Model 95 DO probe.

We assumed respiratory and photosynthetic quotients of 1 when converting data from O<sub>2</sub> to C (Biddanda et al. 2001). This assumption may have led to underestimation of benthic primary production because of anoxic metabolism (Cotner et al. 2004), but the sandy, low organic-matter characteristics of the sediments where we did incubations probably decreased the significance of anaerobic processes. We estimated areal fluxes in the water column by averaging duplicate measurements and multiplying by the water-column depth. We estimated R, GPP, and NEP for the water column and benthos by multiplying by 24 (R) or 12 h (GPP and NEP).

*Biomass (chlorophyll *a*).*—We filtered triplicate samples from each site in situ through Whatman GF/F glass fiber filters, froze them, and later extracted chlorophyll *a* in 90% acetone prior to spectrophotometric measurement (Wetzel and Likens 1991). We collected benthic chlorophyll *a* samples in triplicate with a shallow corer (1.3 cm) at a depth between 0.7 and 1 m. We placed sediments in a Petri dish and froze them until chlorophyll *a* extraction and spectrophotometric analysis. We corrected all chlorophyll *a* values for phaeophytin *a*. Organic matter content of the sediments was determined as the % ash-free dry mass (APHA 1992).

*Nutrient concentrations.*—We gently filtered water samples through Whatman GF/F glass fiber filters and measured NH<sub>4</sub>, NO<sub>3</sub>/NO<sub>2</sub>, SRP, and SiO<sub>3</sub> concentrations using an autoanalyzer and colorimetric assays (APHA 1992). Detection limits achieved with the Technicon II Autoanalyzer were 0.089 μM-NO<sub>3</sub>, 0.009 μM-NO<sub>2</sub>, 0.035 μM-NH<sub>4</sub>, 0.161 μM-urea, 0.024 μM-PO<sub>4</sub>, and 0.071 μM-SiO<sub>3</sub>. In addition, we report values for dissolved inorganic N (DIN), which is the sum of NO<sub>3</sub>, NO<sub>2</sub>, and NH<sub>4</sub>.

*Chemical fluxes.*—We calculated chemical fluxes of nutrients to or from the sediments using the equations of Dollar et al. (1991). These equations are based on the volume of the chamber and changes in nutrient concentrations. All fluxes (DO, SRP, and NH<sub>4</sub>) were corrected for water-column changes measured in BOD bottles. Water-column fluxes were subtracted from the total chamber flux for each solute, yielding estimates for sediment-only fluxes.

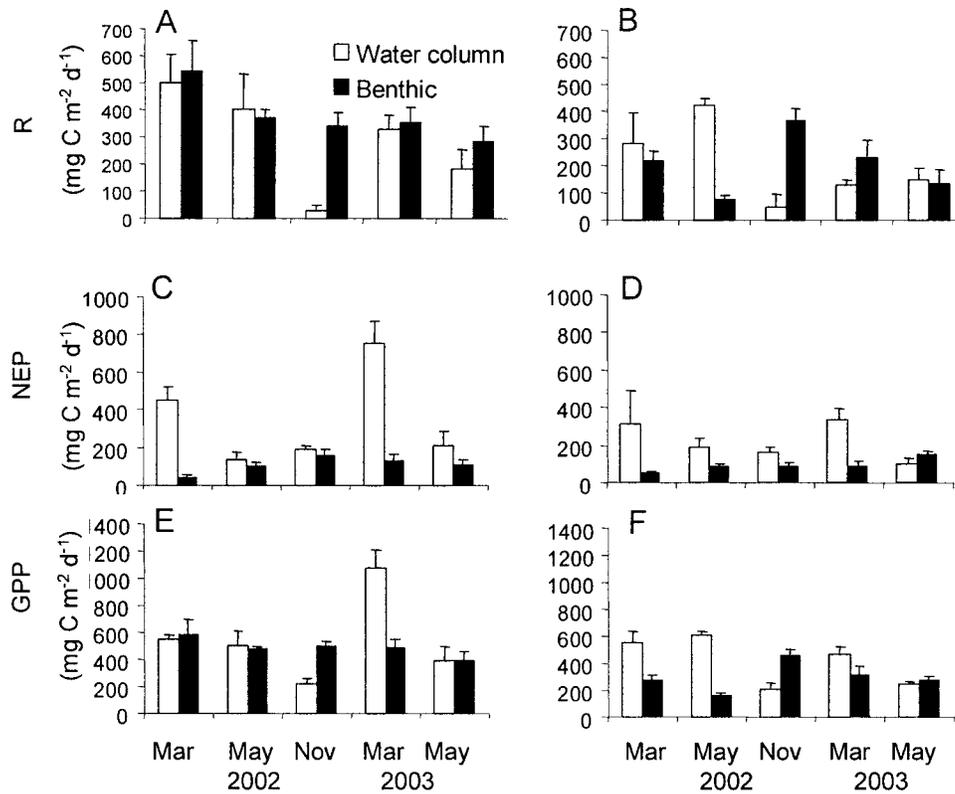


FIG. 1. Mean (+1 SE) respiration (R) (A, B), net ecosystem production (NEP) (C, D), and gross primary production (GPP) (E, F) at lagoon and river sites, respectively.

*Statistical analyses.*—We used analysis of variance (ANOVA) to compare variables between lagoon and river sites and between seasons. Seasonal trends were strong over the period during which we conducted this study, but the study lasted only 1.5 y. We used standard least-squares regression to examine the relationship between nutrients and productivity variables (NEP, GPP, and R). We did all statistical analyses with Systat (version 10.0, Systat Software, Point Richmond, California), and we used  $p = 0.05$  as a benchmark for statistical significance.

**Results**

*Production and biomass*

Water-column R varied seasonally and spatially (Fig. 1A, B). Mean rates were slightly higher in lagoons than in the river (287 vs 207 mg C m<sup>-2</sup> d<sup>-1</sup> in lagoons and river, respectively,  $p < 0.05$ ; Fig. 1A, B), but rates in both habitats were highest during the low-water period (March) and much lower during the falling-water period (November; 29 and 49 mg C m<sup>-2</sup> d<sup>-1</sup> in lagoons and the river, respectively). Decreased R contributed to increased NEP efficiencies during the falling-water period (87% and 77% in the lagoons and river, respectively) relative to other times. These high

production efficiencies also were reflected in high production:biomass (P:B) ratios during the falling-water period. Daily P:B ratios varied from ~0.1 to 9, with higher rates observed in the benthos than in the water column and higher values in November 2002 and May 2003 than during other seasons (Table 1).

Total NEP (benthic + water-column) averaged 447 mg C m<sup>-2</sup> d<sup>-1</sup> in the lagoons and 315 mg C m<sup>-2</sup> d<sup>-1</sup> in the

TABLE 1. Production: biomass (P:B) ratios in the water column and benthos in the Cinaruco. Data were determined from water-column production and chlorophyll *a* levels. A 100:1 C:chlorophyll *a* ratio was assumed when estimating algal biomass.

Habitat	Date	Water	Benthic
Lagoons	March 2002	0.09	0.09
	May 2002	0.21	0.14
	November 2002	0.65	1.59
	March 2003	0.16	0.95
	May 2003	0.77	3.81
River	March 2002	0.38	0.32
	May 2002	0.62	0.57
	November 2002	0.67	5.83
	March 2003	0.32	1.41
	May 2003	1.61	9.00

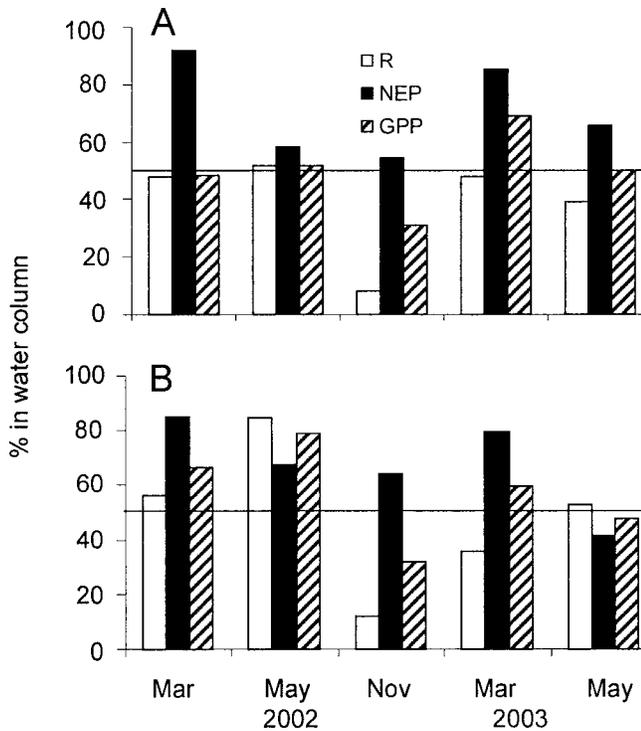


FIG. 2. Percentage of respiration (R), net ecosystem production (NEP), and gross primary production (GPP) that occurred seasonally in the water column of lagoons (A) and the river (B) seasonally. The remainder R, NEP, and GPP occurred in the benthos, so any value >50% indicates that water-column processes exceeded benthic processes.

river over the study period. NEP was always positive, indicating that the shallow littoral area where measurements were made was autotrophic. NEP was more variable in lagoons than in river sites (range, lagoons: 238–882 mg C m<sup>-2</sup> d<sup>-1</sup>, river: 254–426 mg C m<sup>-2</sup> d<sup>-1</sup>; Fig. 1C, D). Lowest values for NEP were observed during the rising- and falling-water periods (May and November) in both habitats, and the highest values were observed in the low-water period (March 2002 and 2003).

On an annual basis, 61% of GPP was lost through R, leaving 39% for transfer to higher trophic levels or export (either as burial or movement downstream). R typically was a bigger sink for GPP in sediments than in the water column (60 vs 51%), presumably because of accumulation of organic matter in the sediments; absolute areal R rates also were higher in sediments than in the water column (665 mg C m<sup>-2</sup> d<sup>-1</sup> in lagoons vs 411 mg C m<sup>-2</sup> d<sup>-1</sup> in the river). However, these littoral sediments had relatively low organic matter content. Sediment organic content was only 0.47% in the lagoons and 0.17% in the river, perhaps reflecting high rates of decomposition, resuspension, and downstream or pelagic transport of organic matter.

A high % of NEP occurred in the water column, even in the shallow regions of this unproductive river system. In lagoons, >3× as much NEP occurred in the water column as in the benthos (349 vs 108 mg C m<sup>-2</sup> d<sup>-1</sup>; Fig. 2A), and, in the river, ~2× as much NEP occurred in the water column as in the benthos (221 vs 94 mg C m<sup>-2</sup> d<sup>-1</sup>; Fig. 2B). Benthic NEP was similar in lagoons and the river sites, but water-column NEP was much higher in lagoons than in river sites. In many cases, NEP was higher in the water column because R consumed less of the GPP in the water column than in the sediments (Fig. 1A–F). R was ~39 to 47% of GPP in the water column (higher in the river) and ~68 to 78% of GPP in benthos (higher in lagoons). Lagoons probably have higher R in sediments because organic matter content is higher there.

Regression analyses indicated that temperature correlated with water-column R and GPP, but not NEP, although NEP was typically higher at higher temperatures (Fig. 3A–C). Small but consistent changes in temperature (Fig. 4A) were associated with highest GPP and R observed in the low-water period. The temperature pattern was very similar to that of ambient DO concentrations (Fig. 4B) and conductivity (Fig. 4C), both of which were associated with higher water-

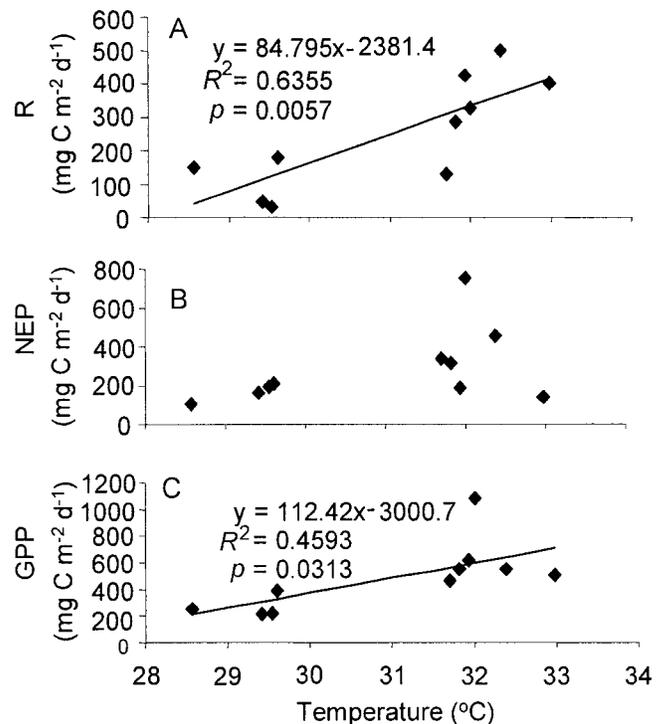


FIG. 3. Regressions for water-column respiration (R) (A), net ecosystem production (NEP) (B), and gross primary production (GPP) (C) with temperature at river and lagoon sites. Regression lines and statistics are shown only for significant relationships.

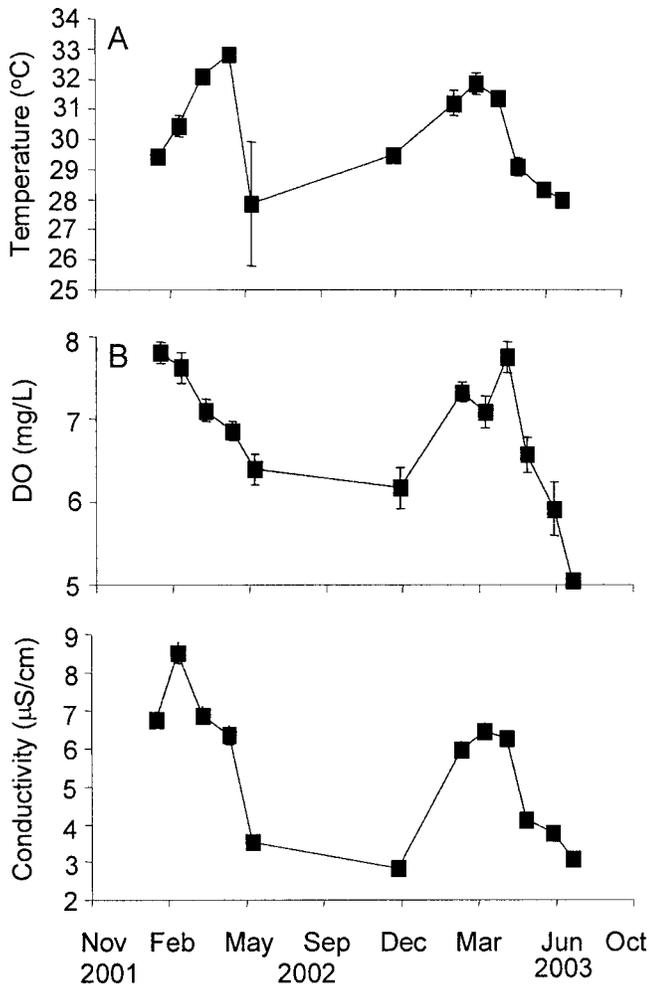


FIG. 4. Mean ( $\pm 1$  SE) temperature (A), dissolved O<sub>2</sub> (DO) (B), and conductivity (C) at river and lagoon sites.

column NEP during the low-water period. Benthic NEP, GPP, and R were not significantly related to temperature (data not shown). The strongest relationship was between benthic NEP and temperature ( $p = 0.066$ ).

Water-column chlorophyll *a* levels were  $>2\times$  greater in the lagoons than in the river sites (4.7 and 2.2 µg/L in the lagoons and river, respectively; Montoya et al. 2006). The same pattern was observed for benthic chlorophyll *a* levels (2.7 and 0.8 mg/m<sup>2</sup> in the lagoons and river, respectively). Chlorophyll *a* levels in the water column and the benthos were higher during the low-water period than the high-water period. Peak water-column chlorophyll *a* levels occurred from the end of March to early May 2002 (6.6–6.8 µg/L) and at the end of March 2003 (10.4 µg/L) (Montoya et al. 2006). Low values occurred in May to July in both years, with lowest values occurring in 2003 (0.42–0.99 µg/L). Benthic chlorophyll *a* levels showed the same seasonal pattern with lower variance at river sites than at lagoon sites.

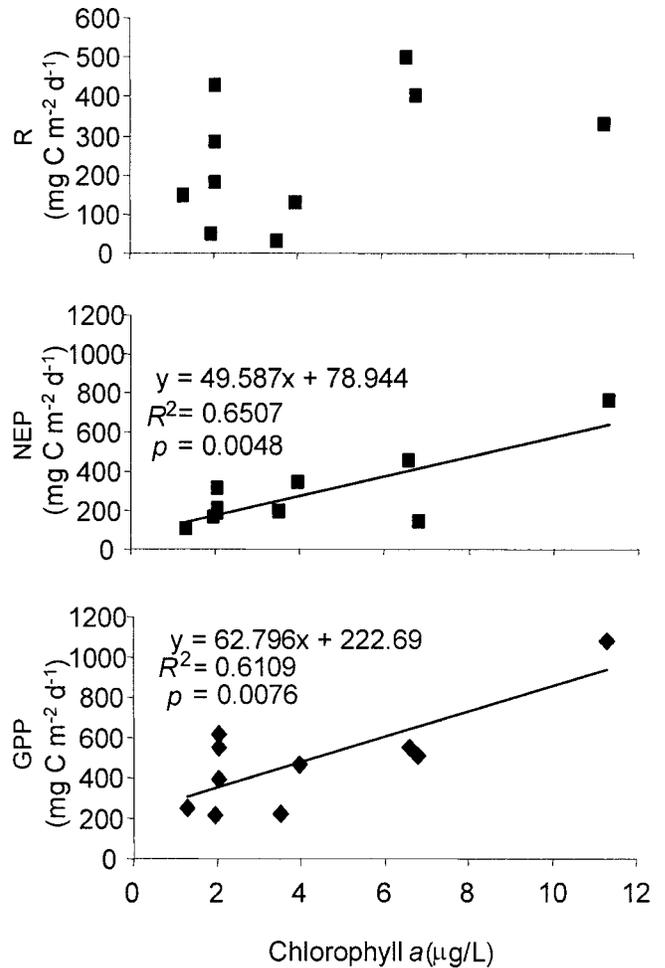


FIG. 5. Regressions for water-column respiration (R) (A), net ecosystem production (NEP) (B), and gross primary production (GPP) (C) with chlorophyll *a* at river and lagoon sites. Regression lines and statistics are shown only for significant relationships.

The relationship between water-column R and chlorophyll *a* was not significant (Fig. 5A), probably because a large part of R in unproductive ecosystems such as this is microbially mediated (Cotner and Biddanda 2002). However, water-column NEP and GPP were significantly related to chlorophyll *a* levels (Fig. 5B, C). Benthic NEP, GPP, and R were not significantly related to chlorophyll *a* levels (data not shown). The strongest relationships were between benthic R and chlorophyll *a* ( $p = 0.087$ ), and benthic GPP and chlorophyll *a* ( $p = 0.072$ ).

*Nutrient concentrations and fluxes*

Nutrient concentrations in the water column were more affected by season than habitat. Mean annual nutrient concentrations did not differ between the 2

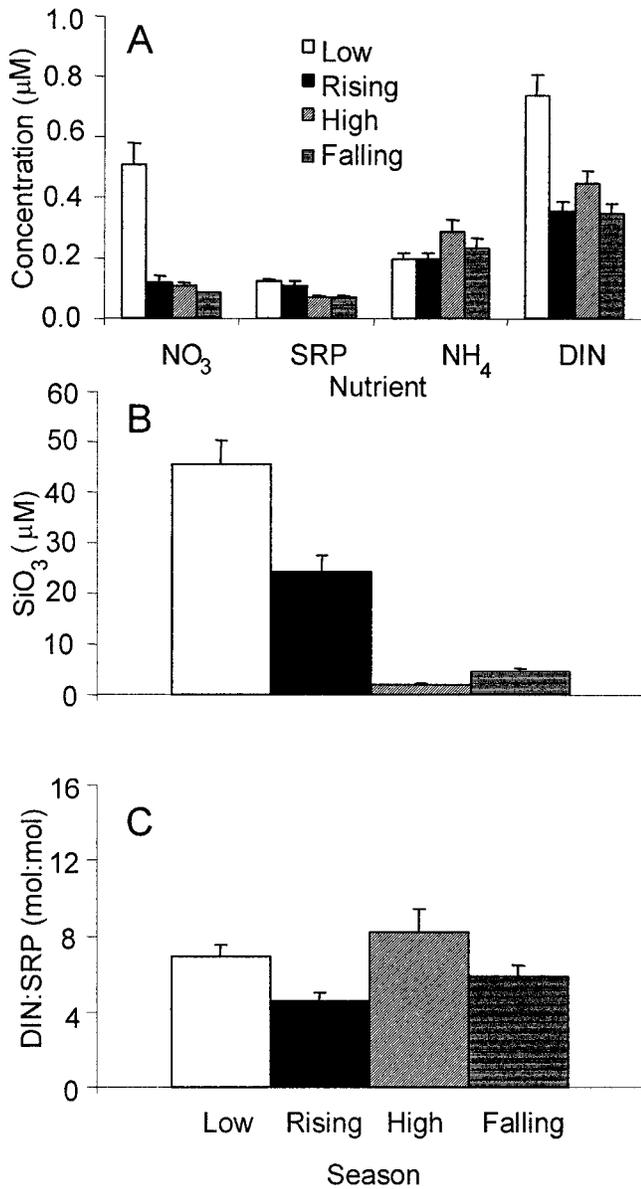


FIG. 6. Mean (+1 SE) seasonal concentrations of NO<sub>3</sub>, soluble reactive P (SRP), NH<sub>4</sub>, and dissolved inorganic N (DIN, NO<sub>3</sub> + NO<sub>2</sub> + NH<sub>4</sub>) (A), SiO<sub>3</sub> (B), and nutrient ratios (C) at river and lagoon sites combined.

habitats, but nutrient concentrations in both habitats were significantly higher during the low-water period than at other times of the year (Fig. 6A, B). Concentrations of all nutrients decreased as the high-water period began, but the changes in concentrations were relatively small for N and P (<0.5 μM; Fig. 6A). SiO<sub>3</sub> concentrations decreased by nearly 200 μM at some sites, and mean decreases were >40 μM (Fig. 6B). Despite this strong seasonal pattern in nutrient concentrations, the mean DIN:SRP ratio did not change significantly among seasons (Fig. 6C).

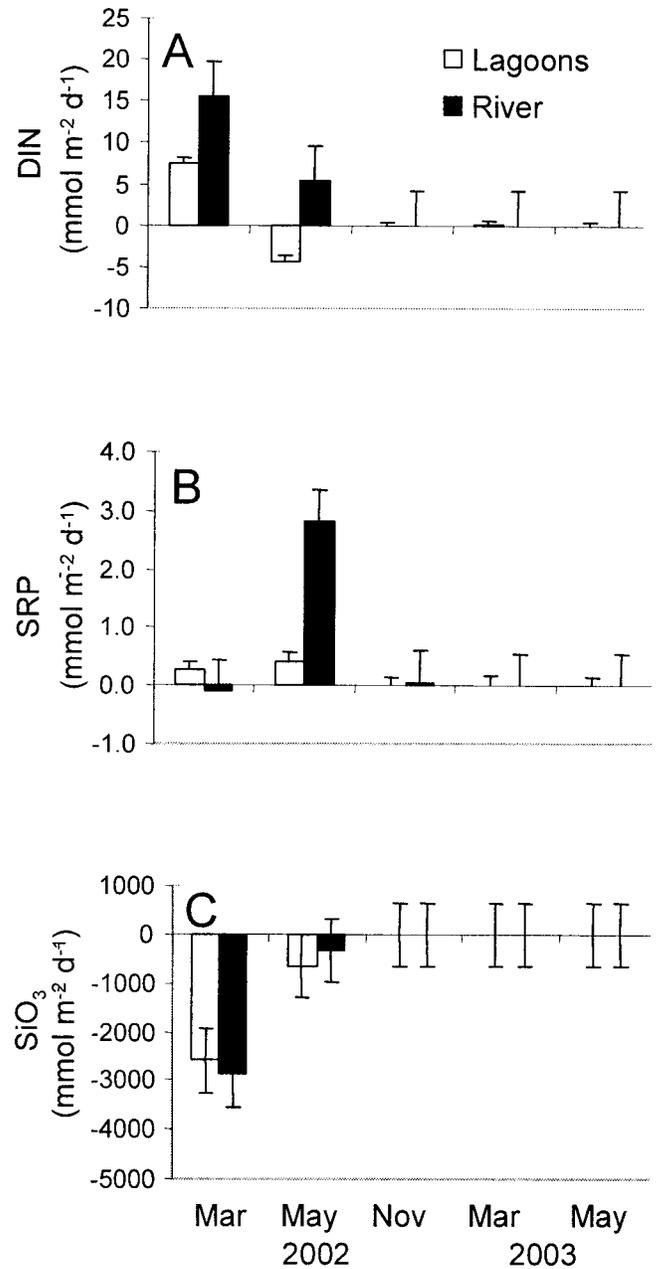


FIG. 7. Mean ( $\pm 1$  SE) benthic fluxes of dissolved inorganic N (DIN = NO<sub>3</sub> + NO<sub>2</sub> + NH<sub>4</sub>) (A), soluble reactive P (SRP) (B), and SiO<sub>3</sub> during dark benthic chamber deployments. A negative value indicates a net flux into the sediments.

Nutrient fluxes from sediments were highly variable between habitats and seasons (Fig. 7A–C). We measured fluxes from sediments in both ambient-light and dark chambers. However, the fluxes under ambient-light conditions were extremely low and often negative (data not shown). Such low rates probably reflected the fact that measurements were done at relatively high light levels (~40% or more of surface light given Secchi

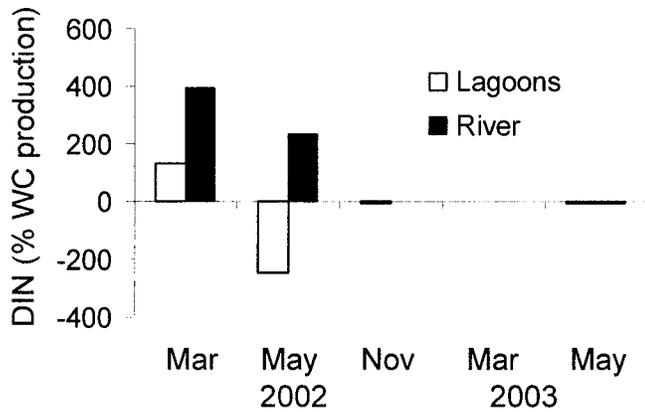


FIG. 8. The importance of dissolved inorganic N (DIN) in fueling water-column (WC) production seasonally. A 6.6:1 C:N ratio (Redfield 1958) was assumed to estimate the % of water-column production the N flux to the water column could support (see text for explanation).

depths of  $\sim 1$  m) with positive benthic NEP. Nutrient fluxes under dark conditions were also low, indicating that the sediments were not an important source of nutrients fueling water-column production. Significant fluxes out of the sediments were observed only during low- and rising-water periods, when both SRP and DIN fluxes generally were positive (Fig. 7A, B). However,  $\text{SiO}_3$  fluxes were strongly negative (into the sediments) during the low- and rising-water periods (Fig. 7C), probably reflecting reverse  $\text{SiO}_3$  weathering (Michalopoulos and Aller 2004).

This system was probably limited by the availability of N, so we examined the importance of inorganic N fluxes to water-column NEP (Fig. 8). DIN fluxes out of the sediments were important to river water-column NEP only in 2002 under conditions of low and rising water. Most (58–100%) DIN fluxes were a result of movement of  $\text{NH}_4$  across the sediment–water interface. High DIN fluxes out of the sediments were observed during the low-water period in lagoons, but DIN fluxes were negative during the rising-water period, perhaps reflecting increased rates of nitrification/denitrification in the sediments at that time.

### Discussion

Our study is one of the first to make productivity measurements for both water-column and benthic habitats in an oligotrophic tropical river. Our measurements were focused on littoral zones of the Cinaruco because these extensive shallow areas dominate the landscape and have highest light penetration and autotrophic production. In addition to providing data on production at the base of this species-rich ecosystem, we wanted to understand processes that generate

temporal and spatial variability in primary production. Our results indicate that: 1) productivity in the shallow regions of this nutrient-poor river is high and net autotrophic, 2) much of the primary production, even in shallow areas, is located in the water column, 3) lagoons are more productive than the main river channel, but the differences between these habitats are not great, 4) this ecosystem is probably most strongly limited by N, and 5) consumers do not appear to have strong effects on algal productivity and nutrient dynamics at the base of the food web.

An important question is how well the measurements we made in the shallow regions of this ecosystem represent the entire system. The lagoons in our study remained connected to the main channel, had length:width ratios  $>5$ , and were formed through riverine scouring processes. Hamilton and Lewis (1990) classified such floodplain lakes in the Orinoco Basin as channel lakes. Channel lakes have steeper sides than depression lakes (dish lakes; Hamilton and Lewis 1990). However, during much of the year (June–September), floodwaters of the Cinaruco are dispersed over the low-gradient savannah, providing a very large littoral surface area (Montoya et al. 2006). Furthermore, high transparency (Secchi depths of 1–2 m; Montoya et al. 2006) in the river and lagoons increases the relative significance of littoral development. So, our measurements were probably representative of a large portion of the riverine system, but because we did not examine processes in the deeper regions, our conclusions regarding net auto- and heterotrophy are restricted to these littoral regions.

### Production dynamics

Our measurements of NEP were always positive, and measurements of GPP were surprisingly high for such a nutrient-poor system. Most rivers are net heterotrophic because of high inputs of allochthonous organic matter (Mulholland et al. 2001). The Cinaruco is probably net heterotrophic as well, but we did not measure GPP and R in the pelagic regions. Nonetheless, we know that significant quantities of terrestrial organic matter are transported into the Cinaruco (Roelke et al. 2006), and this material fuels significant levels of R in the pelagic region of temperate and tropical rivers (Bunn et al. 1999, Mulholland et al. 2001, Richey et al. 2002, Thorp and Delong 2002). However, most of the terrestrial organic matter is recalcitrant and nutrient-poor (Thorp and Delong 2002), so it probably makes little contribution to higher trophic level production.

Terrestrial organic matter may make important contributions to riverine respiration, but autochthonous production seems to be more important for

maintaining food webs. The RPM (Thorp and Delong 1994) suggests that higher trophic levels in river food webs rely more heavily on autochthonous than allochthonous production because autochthonous production is more labile and has higher nutrient content than allochthonous production (Thorp and Delong 1994). In the Orinoco and the Cinaruco rivers, stable-isotope measurements of foodweb components support this argument (Lewis et al. 2001, Jepsen and Winemiller 2002).

Total annual NEP in littoral areas of the Cinaruco river channel and lagoons averaged  $141 \text{ g C m}^{-2} \text{ y}^{-1}$ , and GPP was  $320 \text{ g C m}^{-2} \text{ y}^{-1}$ . Few such measurements have been made in rivers in the tropics. Those measurements that have been made in other tropical rivers and riverine lakes typically have yielded values similar to or lower than ours (Conde 1996, Bunn et al. 1999), and our measurements are high when compared to water-column measurements made in other rivers in the Orinoco Basin. The mainstem Orinoco has lower water-column algal biomass ( $<0.5 \text{ } \mu\text{g/L}$  chlorophyll *a*) and NEP than the Cinaruco (Lewis 1988). However, many of Lewis's (1988) measurements were made in blackwater systems draining the Guiana Shield. Productivity rates in the Apure River (whitewater) were an order of magnitude lower than those we measured. Furthermore, our values of R ( $0\text{--}9.5 \text{ } \mu\text{M O}_2/\text{h}$ ) typically were higher than those measured in the Amazon ( $0.61\text{--}1.96 \text{ } \mu\text{M O}_2/\text{h}$ ; Devol et al. 1987, Benner et al. 1995). Most certainly, the reasons for these discrepancies have to do with the fact that these other studies were performed in the pelagic region of large rivers, whereas we concentrated our efforts in shallow littoral areas where rates are probably highest.

A survey of North American streams showed that these systems had GPPs that were very similar to those measured in our study ( $\sim 10\text{--}100 \text{ g C m}^{-2} \text{ y}^{-1}$ , assuming a 1:1 respiratory quotient; Mulholland et al. 2001). All except one of the streams surveyed by Mulholland et al. (2001) had NEPs that were negative, i.e.,  $\text{GPP} < \text{R}$ . In Mulholland et al.'s (2001) study, whole-river metabolism was examined using open-system diurnal  $\text{O}_2$  changes, whereas our benthic-chamber study targeted the productive shallow areas of the river and lagoons. Our results suggest that, despite relatively low nutrient levels in the Cinaruco Basin, high rates of primary production are maintained in shallow regions of the river. These high rates of production yield important C sources fueling secondary production and could support the high diversity and abundance of benthic feeding fishes in these rivers.

Furthermore, high net productivity in the littoral zone of the Cinaruco suggests a potential for lateral transport of organic matter from these regions to the

pelagic region. This littoral organic matter could be perceived as allochthonous inputs via net heterotrophy in the main channel using the diel  $\text{O}_2$  method. Lateral transport of organic matter might be mediated through movement of organisms (e.g., fish) or by contraction of the river between high- to low-water conditions. The importance of these mechanisms should be examined in future work.

Studies in the Neotropics and in the Orinoco Basin, in particular, provide evidence for the argument that autochthonous primary production supports most of the higher trophic levels. Analyses of lower Orinoco food webs indicated that in situ primary production is an important source of C, despite isotopic signatures of particulate organic C ( $-30$ ) that suggested high inputs of terrestrial matter (Tan and Edmond 1993). Furthermore, particulate C from terrestrial habitats and macrophytes makes up 98% of the organic matter available to organisms in Orinoco floodplain systems, but isotopic signatures suggest that the most important food sources are phytoplankton and periphyton (Hamilton et al. 1992, Lewis et al. 2001).

*Relative importance of water-column vs benthic production.*—The fact that water-column NEP was  $\sim 3\times$  that of the benthos suggests that a considerable amount of in situ production supporting food webs is planktonic. Certainly, the importance of planktonic processes is even more profound in deeper, open-water regions of the river (Fourqurean et al. 1997, Cotner et al. 2004), so we were surprised that planktonic production was so important in these shallow regions. Nonetheless, planktonic biomass probably is an important component maintaining metazoan production directly through grazing or indirectly after plankton enters the detrital food web. Much of the material that accumulates on the sediments in littoral areas in the Cinaruco probably is planktonic biomass that falls to the sediments during nonturbulent periods or consists of resuspended organic sediments. Given the abundance of detritus-feeding fishes in tropical rivers (Roman and Tenore 1984, Mann 1988, Winemiller 1990, Flecker 1992, Duque et al. 1998, Rosemond et al. 2001), it seems probable that detrital export from the water column is a significant biogeochemical flux.

However, we really do not know the relative importance of benthic vs planktonic biomass production in supporting higher trophic levels in this system. Some studies in the Orinoco and Amazon Basins have shown that benthic production is an important source of organic matter to higher trophic level organisms (Hamilton et al. 1992, Forsberg et al. 1993). Hecky and Hesslein (1995) observed preferential consumption of benthic production by primary consumers among lakes at different latitudes despite higher rates of

production in plankton. Support for the view that benthic production is important is provided by our data showing that benthic algal biomass turned over at faster rates than planktonic biomass (Table 1). However, other studies have concluded that planktonic biomass is more important than benthic biomass for supporting secondary production (Araujo-Lima et al. 1986).

*Lagoons vs rivers.*—Our results demonstrated that the riverine lagoons are important regions of high productivity in this nutrient-poor ecosystem. Riverine backwaters are important to fish production in tropical and temperate ecosystems (Welcomme 1979, Ward et al. 1999, Winemiller et al. 2000). In the present work, differences in algal biomass between the 2 habitats were pronounced, and differences in R, NEP, and GPP between habitats were similar to differences in algal biomass, but less pronounced. On average, lagoon sites had more standing algal (planktonic and benthic) biomass than did river sites (Montoya et al. 2006), probably because of higher loss rates or lower nutrient concentrations in the river sites. Water residence times and particle sedimentation in these 2 habitats probably account for most of the biological differences. Shorter residence times in the river should increase plankton loss rates and decrease the settling velocity. As a consequence, sediments have less organic matter and lower nutrient content to support benthic and water-column production in the river than in the lagoons. Furthermore, physical disturbance of sediments can negatively affect productivity. In the Amazon, benthic primary production was highest in the least physically disturbed sediments (Alongi and Robertson 1995). In estuaries, water residence time is a key variable affecting nutrient and planktonic production dynamics, with higher autotrophic production typically occurring at longer residence times (Smith and Veeh 1989, Smith and Hollibaugh 1993). In a northern-temperate floodplain system, longer residence times coincided with periods of high autotrophic production, similar to our findings (Tockner et al. 1999). Therefore, the hydrological processes that are responsible for the strong temporal patterns that we observed (higher NEP during low- and rising-water periods) are probably responsible for many of the differences between the river and lagoon habitats because of longer water residence times in lagoons (Montoya et al. 2006). Supporting this argument, hydrological differences between the 2 habitats were minimized during the high-water period, and this period is also when differences in net production and algal biomass were minimized between the 2 habitats (Figs 1, 2).

### Nutrients

Dissolved nutrient levels were typically very low in the Cinaruco. However nutrient levels had a strong temporal pattern in which nutrient concentrations, especially  $\text{SiO}_3$ , were highest during the low-water period. We also found low dissolved N:P ratios (<8:1 mol:mol), which suggests that N is likely to limit NEP in this system. In addition, nutrient fluxes from sediments typically were not an important N source to the water column (Fig. 8). The only period when we observed significant positive fluxes was during low water in 2002, perhaps indicating that sediment fluxes may be partly responsible for increased nutrient concentrations in the water at that time.

It is not surprising that this riverine ecosystem is probably N-limited. In Amazon floodplain lakes, dissolved N:P ratios are low (typically <15:1), but ratios are higher in blackwater rivers than in rivers draining the Andes (Forsberg et al. 1988). In floodplain lakes of the lower Orinoco Basin, dissolved N:P ratios are higher (~15:1) than those that we measured in the Cinaruco, but measurements in the Apure River were similarly low (7:1). Hamilton and Lewis (1990) found an average DIN:SRP ratio of 13:1 in lower Orinoco floodplain lakes. Higher values in the lower Orinoco are probably influenced by higher N:P ratios in waters flowing over the Guiana Shield. In a N-limited Venezuelan piedmont stream, DIN levels were similar to but slightly higher than those in the Cinaruco (<4  $\mu\text{M}$ ), with dissolved N:P ratios of 8 to 15 during the low-water period (Flecker et al. 2002). Furthermore, algivorous and detritivorous fishes actually increased the potential for N-limitation, presumably by selecting for grazer-resistant algae.

N-limitation is common in tropical ecosystems, especially savannas (van Breman and de Wit 1983, Vitousek and Howarth 1991) and rivers (Downing et al. 1999). The Cinaruco Basin is a strongly weathered landscape with high losses of N because of its high mobility (Vitousek and Howarth 1991, Austin and Vitousek 1998). Furthermore, fires occurring in the llanos could contribute to N-limitation because pyrodenitrification contributes to high N losses as N volatilizes from burned regions (Medina and Silva 1990, Vitousek and Howarth 1991, Sanhueza and Crutzen 1998, Downing et al. 1999, D'Antonio et al. 2001).

### Correlations with R, NEP, and GPP

Our measurements indicated that R typically consumed ~50 to 75% of GPP and was an important sink for GPP in the Cinaruco. R losses were positively correlated with temperature and GPP. In their survey

of several North American streams, Mulholland et al. (2001) found that stream R was best predicted by SRP and watershed area rather than GPP. In the Cinaruco, R, NEP, and GPP were not correlated with nutrient concentrations. Given the strong nutrient limitation and low nutrient concentrations, this result is not surprising. Annual and interannual fluctuations in nutrient concentrations are small because any increased loading or regeneration is rapidly consumed by phytoplankton, periphyton, and bacteria.

Several studies have demonstrated that R can be strongly correlated with temperature, but most of this work has been done in temperate systems (del Giorgio and Peters 1994, Smith and Kemp 1995, del Giorgio et al. 1997, Biddanda et al. 2001, Enquist et al. 2003). Our work suggests that temperature strongly affects respiratory losses despite changes in mean monthly temperatures of only 5°C. However, correlations between R and temperature may be spurious because GPP also was correlated with temperature (Fig. 3). In fact, GPP increased more with temperature than R did, thereby contributing to high rates of NEP and, presumably, increased autotroph biomass (although our NEP–temperature correlation was not statistically significant).

The water-column values of R during the falling-water period in November 2002 were notably low at both lagoon and river sites (Fig. 1). A similarly low R was observed in the Amazon during high water (Benner et al. 1995). The cause of such low values of R during the low-water period is unclear, but one possibility is that growth efficiencies increased (Benner et al. 1995). The high production:biomass (P:B) ratios (Table 1) in November 2002 are consistent with this interpretation. Nutrient levels were relatively low during high water, probably because of dilution, but algal and (presumably) bacterial biomass were also low. In other systems, highest growth efficiencies typically occur when planktonic biomass is low (del Giorgio and Cole 1998, Pakulski et al. 1998, Biddanda et al. 2001), perhaps because of high substrate availability and decreased competition.

### *Seasonality*

Consistent with other studies of tropical riverine systems (Forsberg et al. 1988, Lewis 1988, Forsberg et al. 1993, Castillo 2000), the highest nutrient concentrations and productivities occurred during the low-water phase. We hypothesized that top–down effects on benthic periphyton would be particularly strong during this period because of high abundances of benthivorous fishes. The fact that nutrient levels increased during this period is consistent with this

hypothesis, but planktonic and benthic chlorophyll *a* levels also increased, a result that suggests that grazing losses were not important. In contrast, experimental work (Winemiller et al. 2006) suggested that grazers could have significant effects on benthic organic matter and chlorophyll *a* on firm substrates. Two factors could explain this apparent paradox. First, standing stocks of benthic chlorophyll *a* would have been even greater in the absence of benthivorous algivores, as indicated by field experiments that excluded grazers (Winemiller et al. 2006). Second, effects of grazers could have been patchily distributed and biased toward hard substrates within littoral areas. Measurements in the current study might have been biased to areas with low grazing pressure because they were made over soft substrates. Nonetheless, given the uniform appearance of littoral-zone substrates, particularly within the river channel, the latter hypothesis seems less likely than the former.

Given the low nutrient levels in this system, processes at the bottom of the food web were probably most influenced by hydrological processes that affected nutrient loading. In the Amazon Basin, higher nutrient concentrations observed at high water have been attributed to either physical (hydrologic concentration, sediment resuspension and nutrient release, or atmospheric deposition) or biological interactions (increased mineralization, increased N-fixation) (Forsberg et al. 1988). In the Cinaruco, physical processes probably are important to dissolved nutrient concentrations given that: 1) during the low-water period, mineralization (R) increased but not as much as GPP, and 2) we observed increases in all nutrients (rather than just N) during the low-water period. In addition, atmospheric deposition of nutrients, including ash deposition from fires, also has been reported as an important nutrient source during the low-water period (Sanhueza and Crutzen 1998). The potential significance of atmospheric deposition and hydrologic concentration effects is further emphasized by the low nutrient fluxes from the sediments in our system (Fig. 7).

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