References

BERMAN, T., AND W. RODHE. 1971. Distribution and migration of *Peridinium* in Lake Kinneret. Mitt. Int. Ver. Theor. Angew. Limnol. 19, p. 266–276.

BLASCO, D. 1978. Observations of the diel migration of marine dinoflagellates of the Baja California coast. Mar. Biol. **46:** 41–47.

EPPLEY, R. W., O. HOLM-HANSEN, AND J. D. STRICKLAND. 1968. Some observations on the vertical migrations of dinoflagellates. J. Phycol. **4:** 333–340.

FREMPONG, E. 1984. A seasonal sequence of diel distribution patterns for the planktonic flagellate *Ceratium hirundinella* in an eutrophic lake. Freshwater Biol. **14:** 401–422.

GLIWICZ, Z. M. 1984. Limnological study of Cahora Bassa reservoir with special regard to sardine fishery expansion. FAO, Rome.

———. In press. A lunar cycle in zooplankton. Ecology.

HASLE, G. R. 1950. Phototactic vertical migration in marine dinoflagellates. Oikos **2:** 162–175.

SENFT, W. H., R. A. HUNCHBERGER, AND K. E. ROBERTS. 1981. Temperature dependence of growth and phosphorus uptake in two species of *Volvox* (Volvocales, Chlorophyta). J. Phycol. **17:** 323–329.

SALONEN, K., R. I. JONES, AND L. ARVOLA. 1984. Hypolimnetic phosphorus retrieval by diel vertical migrations of lake phytoplankton. Freshwater Biol. **14:** 431–438.

SIBLEY, T. H., P. L. HERRGESELL, AND A. W. KNIGHT. 1974. Density dependent vertical migration in the freshwater dinoflagellate *Peridinium penardii* (Lemm.) Lemm. fo. *californicum* Javorn. J. Phycol. **10:** 475–477.

SOMMER, U. 1982. Vertical niche separation between two closely related planktonic flagellate species (*Rhodomonas lens* and *Rhodomonas minuta* v. *nannoplanktica*). J. Plankton Res. **4:** 137–142.

TALLING, J. F. 1971. The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. Mitt. Int. Ver. Theor. Angew. Limnol. 19, p. 214–243.

TILZER, M. M. 1973. Diurnal periodicity in the phytoplankton assemblage of a high mountain lake. Limnol. Oceanogr. **18:** 15–30.

Submitted: 15 May 1985
Accepted: 20 November 1985

Limnol. Oceanogr., 31(3), 1986, 653–656

Organic carbon in the Caura River, Venezuela[1]

Abstract—Samples were taken weekly over a 2-year period near the mouth of the Caura River, which drains a large watershed on Precambrian shield covered with tropical moist forest. The concentrations of dissolved organic carbon were essentially static despite a 10-fold seasonal change in discharge. Particulate carbon showed an unexpected but relatively weak inverse relationship to discharge. Yield of total organic carbon (12.3 g C m^{-2} yr^{-1}) was higher than would have been expected from the literature. Yield can be predicted accurately from discharge because of the strong homeostasis in concentration of dissolved organic carbon.

Information on concentrations of organic carbon in rivers throughout the world has become considerably richer over the last 10 years (Degens et al. 1984). Even so, detailed information on organic carbon in large rivers draining tropical moist forest is still very scarce (Schlesinger and Melack 1981). Our 2-year study of the Caura River, a tributary of the Orinoco, provides concurrent measurements of particulate organic carbon, dissolved organic carbon, and discharge for a large river draining undisturbed tropical moist forest.

The Caura River watershed (47,500 km^2) is located between 4° and 8°N lat within Venezuela. The watershed, which is virtually uninhabited, occupies a portion of the Guayana shield, a highly weathered Precambrian formation. The vegetation of the watershed is a mixture of premontane rainforest (29%) with precipitation of about 6,000 mm yr^{-1}, very humid tropical and premontane forest (42%; 3,000 mm yr^{-1}), and humid tropical forest (29%; 2,200 mm yr^{-1}) (Ewel et al. 1976). Average runoff is close to 2,400 mm yr^{-1}.

We sampled the mouth of the Caura at

[1] This work was supported by National Science Foundation grant BSR 83-15410 and by the Venezuelan Ministerio del Ambiente y Recursos Naturales Renovables. J. Meyer and an anonymous reviewer commented on the manuscript.

biweekly intervals between May 1982 and March 1984. On each date, we took four velocity-integrated samples over the cross section of the river with a sampler of the type described by Nordin and Skinner (1977). The samples were taken to a field laboratory at Ciudad Bolivar on the Orinoco River, where they were filtered through preweighed, combusted Whatman GF/C glass-fiber paper (effective pore size ~0.7 μm: Sheldon 1972). The concentration of total particulate material was calculated from the dry weight gain of the filters. Percentage carbon in particulate material was determined for triplicate filter subsamples combusted in a CHN analyzer (Carlo Erba 1106) calibrated with standard orchard leaves (U.S. NBS) and with EDTA. A portion of the filtrate was placed in an ashed glass ampule and the ampule contents were purged of inorganic carbon after addition of phosphoric acid. Persulfate was added to the samples, after which they were sealed and autoclaved. This is considered an efficient means of converting mixed organic species to CO_2 (Strickland and Parsons 1972). Reagent blanks and standards were prepared at the same time by the same method. The CO_2 in the ampules was analyzed on a gas chromatograph (Hewlett-Packard 5840A) in thermal conductivity mode. The amount of soluble organic carbon was computed from the amount of CO_2 in each ampule.

Daily gauge readings on the Caura River, obtained from the Venezuelan Ministerio del Ambiente y Recursos Naturales Renovables, were calibrated against 26 separate discharge measurements made by the Venezuelan government and the U.S. Geological Survey. On the basis of the calibration curve ($r = 0.97$), all gauge readings were converted to discharges. The discharges were then used in computing the total carbon yields for each biweekly interval of the study.

Figure 1 shows the concentrations and yields for dissolved, particulate, and total organic carbon. Even though the Caura is a "blackwater" river, and thus would be expected to have exceptionally high concentrations of dissolved organic carbon (DOC), the mean concentration of DOC (discharge-weighted) is only 3.99 mg liter^{-1}. Discharge-weighted particulate carbon averages 1.09 mg liter^{-1} and thus contributes significantly to total transport.

Total carbon transport for the Caura River is 12.3 g C m^{-2} yr^{-1}, which exceeds that of watersheds >500 km^2 listed in the review by Schlesinger and Melack (1981). Transport for the Caura River is also well above the trend line established by Schlesinger and Melack for the relationship between annual discharge and carbon yield. Thus the unexpectedly low DOC concentrations of the Caura are more than compensated by high runoff.

As shown by Fig. 1, the discharge of the Caura River changes seasonally by a factor of about 10. It is surprising, in view of these large changes in discharge, that there is no relationship between concentration of dissolved organic carbon and discharge ($r = 0.04$, $P > 0.05$). There is a notable but very brief increase of DOC just at the beginning of the rising water that indicates a temporary flushing phenomenon (cf. Brinson 1976), but the dissolved carbon concentrations are otherwise very steady (C.V., 27%).

Particulate organic carbon shows a weak but statistically significant relationship to discharge. The relationship is negative rather than positive, as might have been expected ($r = -0.31$, $P = 0.04$). The concentration of total organic carbon, which is a composite of the dissolved and particulate fractions, shows very low seasonal variation (C.V., 26%), and there is no significant relationship to discharge ($r = -0.12$, $P > 0.05$).

The lack of relationship between discharge and concentration of DOC ensures that the yield of DOC from the Caura River drainage will be almost entirely under the control of discharge. This is illustrated by the yield data in Fig. 1. Over 80% of the variance in export of DOC is explained by discharge ($r = 0.91$, $P < 0.01$). The same is true, although not quite so emphatically, for yield of particulate carbon ($r = 0.52$, $P < 0.01$). The concentrations of dissolved and particulate carbon are significantly but weakly correlated with each other ($r = 0.45$, $P < 0.01$). Total yield of organic carbon, which is the composite of the two concentrations weighted by the discharge, is very tightly related to discharge ($r = 0.92$, $P < 0.01$).

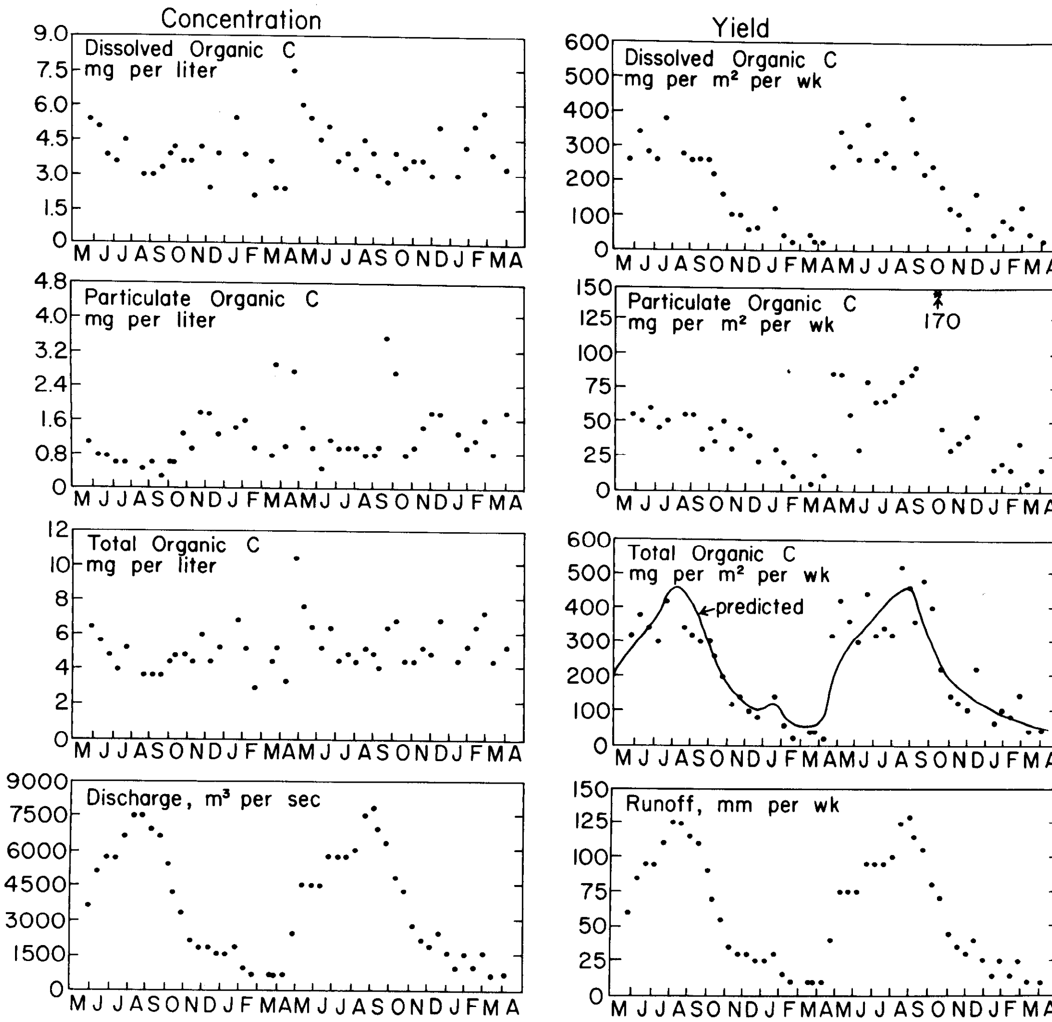

Fig. 1. Concentrations and yields of organic carbon for the Caura River, Venezuela, 1982–1984.

Because of the close relationship between yield of total organic carbon and discharge, it is possible to predict carbon yield quite accurately from discharge on any given date. A least-squares fit was done for the measurements of carbon yield in relation to discharge. The discharge on each date was then used to predict carbon yield on that date, and a smooth line was drawn through these predicted yields as shown in Fig. 1.

When the runoff from a watershed varies a great deal seasonally, concentrations of dissolved substances often vary greatly as well. Dilution is common for major inorganic ions, but DOC or its components may in some watersheds increase in concentration as discharge increases (Lewis and Grant 1979; Schlesinger and Melack 1981; Tate and Meyer 1983). Concentration of particulate material in running waters often increases in relation to discharge because of the greater capacity of faster-flowing, more turbulent water to offset sedimentation. In the Caura River, failure of DOC to show evidence of either dilution or purging over a 10-fold range in discharge suggests that the mature tropical forest buffers the soluble organic carbon pool against runoff. The mechanism by which this could occur is unclear, but one possiblity is that water picks up a refractory organic load in the course of its short passage through the upper organic soil layers and that subsequent residence time in lower, inorganic soil layers is not accompanied by major changes in organic carbon. The slight trend toward declining concentrations of particulate carbon with increasing discharge probably reflects the virtual elimination of erosion in a mature tropical forest occupying flat terrain.

For the Amazon River drainage, Richey et al. (1980) concluded that there is a seasonal homeostasis in yield that can be explained by a tendency of high discharges to be offset by lower concentrations of carbon. This model is not applicable to the Caura River, which shows homeostasis in concentrations rather than yields. However, the Amazon, unlike the Caura, is a mixed water whose sources derive not only from tropical moist forest on flat terrain but also from the Andes. Furthermore, oxidation of organic matter in transit, a major factor over the very long distances of the Amazon main stem, is much less important in the Caura (<10% as indicated by respiration measurements in situ), and the Caura, unlike the Amazon, lacks extensive floodplain.

It is possible that seasonal constancy of organic carbon concentrations is characteristic of waters draining lowland tropical areas of high rainfall and low relief, but the evidence is still very limited. The Caroni River, which drains a portion of the Guayana shield, was sampled on seven dates by Paolini et al. (1983), whose data show large fluctuations in the concentration of DOC (5–17 mg liter^{-1}). However, impoundment of this river upstream of the sampling point may have affected the concentrations. Streams draining inhabited tropical watersheds studied by Lugo and Quinones (1983) showed little change in concentrations of organic carbon with discharge. In general, however, we cannot tell without a broader geographic base whether constancy of organic carbon concentrations is widespread in waters draining tropical moist forest. If it is, phenomenological modeling of carbon flux from mature tropical ecosystems will be easier, but the important underlying mechanisms that might explain constancy are yet to be understood.

William M. Lewis, Jr.
James F. Saunders III

Department of Environmental, Population and Organismic Biology
University of Colorado
Campus Box 334
Boulder 80309

Suzanne N. Levine

Ecosystems Research Center
Cornell University
Ithaca, New York 14853

Franz H. Weibezahn

Universidad Simon Bolivar
Caracas, Venezuela

References

BRINSON, M. 1976. Organic matter losses from four watersheds in the humid tropics. Limnol. Oceanogr. **21:** 572–582.

DEGENS, E., S. KEMPE, AND V. ITLEKKOT. 1984. Monitoring carbon in world rivers. Environment **26:** 29–33.

EWEL, J. J., A. MADRIZ, AND J. A. TOSI. 1976. Zonas de vida de Venezuela, 2nd ed. Sucre, Caracas.

LEWIS, W. M., JR., AND M. C. GRANT. 1979. Relationship between stream discharge and yield of dissolved substances from a mountain watershed. Soil Sci. **128:** 353–363.

LUGO, A., AND F. QUINONES. 1983. Organic carbon export from intensively used watersheds in Puerto Rico. Mitt. Geol. Paleont. Inst. Univ. Hamburg. SCOPE/UNEP Sonderband 55, p. 237–242.

NORDIN, C. F., JR., AND J. V. SKINNER. 1977. Sediment sampling equipment for deep fast currents. Proc. Int. Assoc. Hydraul. Res. **6:** 606–609.

PAOLINI, J., R. HERERRA, AND A. NEMETH. 1983. Hydrochemistry of the Orinoco and Caroni rivers. Mitt. Geol. Paleont. Inst. Univ. Hamburg. SCOPE/UNEP Sonderband 55, p. 223–236.

RICHEY, J. E., J. T. BROCK, R. J. NAIMAN, R. C. WISSMAR, AND R. F. STALLARD. 1980. Organic carbon: Oxidation and transport in the Amazon River. Science **207:** 1348–1351.

SCHLESINGER, W. H., AND J. M. MELACK. 1981. Transport of organic carbon in the world's rivers. Tellus **33:** 172–187.

SHELDON, R. W. 1972. Size separations of marine seston by membrane and glass fiber filters. Limnol. Oceanogr. **17:** 494–498.

STRICKLAND, J. D., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis, 2nd ed. Bull. Fish. Res. Bd. Can. 167.

TATE, C. M., AND J. L. MEYER. 1983. The influence of hydrologic conditions and successional state on dissolved organic carbon export from forested watersheds. Ecology **64:** 25–32.

Submitted: 1 August 1985
Accepted: 9 December 1985