

Basin morphology in relation to chemical and ecological characteristics of lakes on the Orinoco River floodplain, Venezuela

By STEPHEN K. HAMILTON and WILLIAM M. LEWIS, Jr.¹

With 13 figures and 9 tables in the text

Abstract

This study analyzes the relation between chemical and ecological characteristics and basin morphology in lakes on the Orinoco River floodplain of Venezuela. The analysis was based upon measurements of dissolved oxygen, major ions, nutrients, particulates, and chlorophyll-a over an annual cycle for five lakes and upon less frequent samples from 28 lakes. Major ions served as tracers of water sources (river and local rain) to the lakes. The ratio of maximum length to maximum width was used to distinguish lakes during inundation. Channel lakes (length : width > 5) have detectable currents and short water residence times; their chemistry resembles that of the source water, with little change in suspended particulates or in concentrations of labile nutrients, and negligible phytoplankton growth. Dish lakes (length : width < 5) have relatively low rates of water movement and longer water residence times, and deviate in chemistry from the source water because of sedimentation of inorganic particulates, depletion of nitrate, growth of phytoplankton, and depletion of dissolved oxygen. Major ion data indicate that local rainfall was not a detectable source of water to lakes during inundation. During isolation, major ion data show a significant but variable contribution of local waters (rain and runoff) to the water budget of the lakes, which made prediction of lake characteristics difficult. Lake morphology (particularly the ratio of surface area to volume) was just one of several determinants of the importance of local waters to a given lake; other factors included position on the floodplain and the presence of perennial streams. In one lake for which detailed data were available, changes in the intensity of sediment re-suspension during isolation were predictable from wind velocity, effective fetch, and the mean depth of the lake.

Introduction

The lakes of a floodplain typically show considerable chemical and ecological variation, even though they are usually inundated by a common source of river water (WELCOMME 1985, FORSBERG et al. 1988, MARSH & HEY 1989).

¹ Address of the authors: Center for Limnology, Department of Environmental, Population, and Organismic Biology, Campus Box 334, University of Colorado, Boulder, CO 80309 U.S.A.

Present address of St. K. HAMILTON: Department of Biological Sciences, University of California, Santa Barbara, CA 93106 U.S.A.

Much of the variation among lakes is probably caused by differences in lake basin morphology (MELACK 1984). However, few studies have investigated the degree to which the chemical and ecological characteristics of floodplain lakes can be predicted from their morphology. Present classification systems for floodplain lakes are based largely on the origin of the lakes (HUTCHINSON 1957, DRAGO 1976), and may or may not reflect functional characteristics. A classification that links morphology with function would facilitate the extrapolation of results from studies of a statistically valid sample of lakes to the entire floodplain ecosystem. Meaningful extrapolation of this type is becoming increasingly important as the focus of biogeochemical and ecological research on floodplains expands to regional scales.

In this study, we analyze the relationship between basin morphology and chemical and ecological characteristics in lakes on the Orinoco floodplain. The analysis is based upon chemical data taken over an annual cycle for five lakes and upon less frequent samples from 28 lakes.

The Orinoco River and its floodplain

The Orinoco River is the third largest river in the world in terms of discharge to the oceans (average discharge, $36,000 \text{ m}^3 \text{ s}^{-1}$; MEADE et al. 1983). 70% of the drainage basin is located within Venezuela (Fig. 1). Major tributaries along the lower Orinoco include the Meta and Apure rivers, which drain the Andean foothills and savanna to the west, and the Caura and Caroní rivers, which drain the Precambrian Guayana Shield to the south. Although almost half of the water in the Orinoco River originates from the shield region to the south, the Meta and Apure rivers contribute disproportionately to the solute and particulate load of the main channel (LEWIS & SAUNDERS 1989). Detailed information on the chemistry of the Orinoco River and its tributaries can be found in WEIBEZAHN (1985), LEWIS et al. (1987), SAUNDERS & LEWIS (1989), and LEWIS & SAUNDERS (1989).

From the Meta River to the delta, the main channel is fringed by a floodplain covered mostly by forest and permanent waterbodies. This fringing floodplain is seasonally (June—November) inundated by flow from the main channel of the river. Shallow flooding occurs seasonally in large expanses of savanna in the vicinity of the Apure and Meta rivers; these floodplains are of the internal delta type (WELCOMME 1985), and are ecologically and biogeochemically distinct from the Orinoco fringing floodplain (SARMIENTO 1983, SAUNDERS & LEWIS 1988 and 1989). Another distinct floodplain region is found in the Orinoco delta, much of which is affected by tides and seawater and is covered by mangrove forest (VAN ANDEL 1967). Smaller flooded areas are found in the lower reaches of several tributaries, including the Caura River, where the hydrograph closely follows that of the main channel of the Orinoco.

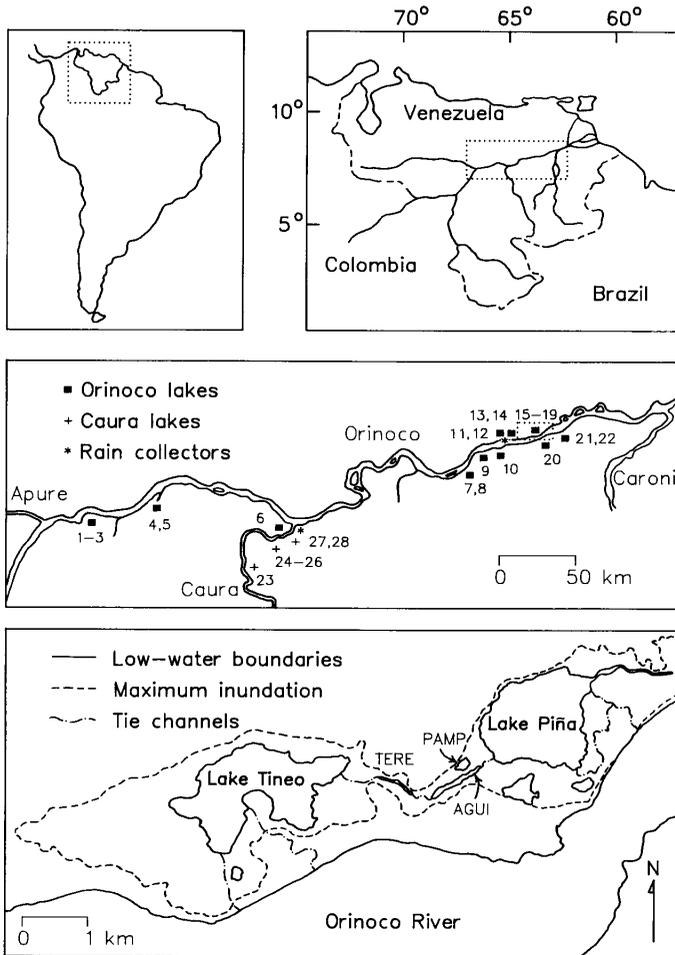


Fig. 1. Location of the study area. The center panel shows the sites for the lake surveys and collection of atmospheric deposition. The lower panel is an enlargement of sites 15–19, five lakes that were sampled intensively for one year. TERE = Lake Terecaya, AGUI = Lake Aguilera, and PAMP = Lake Pámpano.

Seasonal variation of rainfall in the Orinoco basin results in a pronounced annual rise and fall of the river level (Fig. 2). Seasonal inundation of the fringing floodplain is unimodal and typically lasts for 4–6 months, as illustrated by the stage data for a floodplain lake (Lake Tineo) in Fig. 2. With respect to the riverine inundation, HAMILTON & LEWIS (1987) distinguished four hydrological phases in Lake Tineo: filling, through-flow, drainage, and isolation. For present purposes, the filling and through-flow phases are referred to collectively as

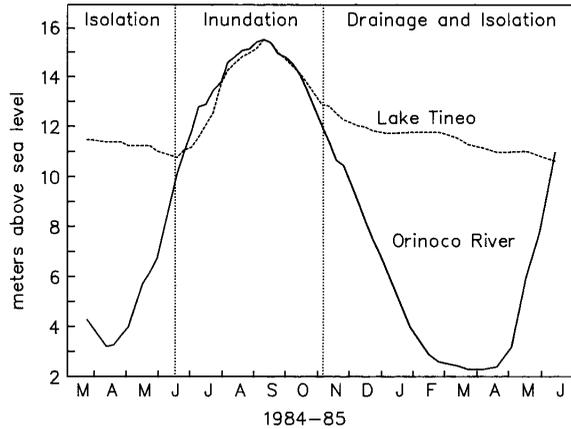


Fig. 2. Hydrographs for the Orinoco River at Ciudad Bolívar and for Lake Tineo, located on the floodplain near Ciudad Bolívar. The river data were provided by the Venezuelan Ministerio del Ambiente y de los Recursos Naturales Renovables.

the inundation phase. For Lake Tineo, the timing of the inundation and isolation phases in 1984–85 is marked in Fig. 2.

Methods

Lake surveys

We sampled 22 sites on the Orinoco fringing floodplain and 6 sites on the fringing floodplain of the Caura River near its confluence with the Orinoco (Fig. 1; Table 1). The Orinoco sites span approximately 400 of the 770 km of the Orinoco River that is bordered by fringing floodplain.

Morphometric characteristics of the sites (Table 2) were measured on maps of 1:100,000 scale, produced by the Venezuelan Dirección de Cartografía Nacional from aerial photography taken between 1968 and 1975. Extensive field work in the floodplain between 1984–88, which has included aerial photography, has shown that lake boundaries on the 1:100,000 maps accurately represent low-water boundaries, corresponding closely to the forested shorelines. During inundation, the boundaries of neighboring lakes often merge as the entire floodplain becomes covered by a continuous sheet of water; low-water lake basins generally remain as open water surfaces bordered by flooded forest. The survey included several forest sites that flood seasonally during inundation and become dry when the river level falls (Piedra Rajada, Caño Masaraca, and Paramuto Forest). At low water, all of the sampling sites were hydrologically isolated, lacking surface-water connections with adjacent lakes and the river.

Effective fetch was measured by the method of the U.S. Army Coastal Engineering Research Center (1977), which accounts for the effect of lake width in reducing the fetch. We measured the length of the central radial, which was aligned with the prevailing wind direction (ENE at Ciudad Bolívar: MARNR 1983), as well as the lengths of radials at 6°-intervals up to 42° from each side of the central radial. The extremely fine particulates that are resuspended in littoral areas of these lakes are likely to be transported throughout the lake before they settle, and we have not observed notable spatial

Table 1. Names, code numbers, acronyms, lake classification, river bank location (left or right), geographic coordinates, and number of sampling dates for the sites sampled in the study. Lakes are classified as dish (D), channel (C), serial dish (SD), or serial channel (SC), as explained in the text.

Lake Name	Reference	Class	Bank	Lat. (N)	Long. (W)	Sampling Dates		
						Inund.	Isol.	
<i>Orinoco lakes</i>								
Castillero	1	CAST	D	R	7°38' 30"	66°09' 00"	3	1
La Teja	2	TEJA	D	R	7°39' 06"	66°08' 30"	3	–
Bartolico	3	BART	D	R	7°38' 30"	66°07' 00"	3	1
La Sapoara	4	SAPO	C	R	7°48' 00"	65°43' 20"	4	–
Caño Uyape	5	UYAP	SC	R	7°48' 00"	65°42' 30"	4	–
Guaipure	6	GUAI	D	R	7°36' 30"	64°56' 00"	2	–
La Esperanza	7	ESPE	C	R	8°01' 00"	63°51' 20"	4	–
Caño Largo	8	CLAR	C	R	8°01' 00"	63°51' 35"	4	–
Maldonado	9	MALD	D	R	8°06' 00"	63°46' 00"	4	1
Piedra Rajada	10	PRAJ	D	R	8°08' 15"	63°36' 45"	4	–
Caño Caramacate	11	CARA	C	L	8°10' 15"	63°37' 00"	4	1
Curita	12	CURI	D	L	8°09' 20"	63°35' 50"	4	1
Playa Blanca	13	PBLA	D	L	8°09' 15"	63°35' 10"	–	1
La Orsinera	14	ORSI	D	L	8°09' 25"	63°34' 30"	14*	2*
Tineo	15	TINE	D	L	8°11' 25"	63°28' 20"	15*	2*
Terecaya	16	TERE	SC	L	8°11' 25"	63°27' 30"	15*	2*
Aguilera	17	AGUI	SC	L	8°11' 25"	63°26' 40"	15*	2*
Pampano	18	PAMP	SD	L	8°11' 40"	63°26' 40"	15*	2*
La Piña	19	PIÑA	D	L	8°12' 15"	63°26' 00"	15*	2*
Palmarito	20	PALM	D	R	8°11' 40"	63°22' 20"	4	1
La Tigra	21	TIGR	D	R	8°11' 40"	63°20' 20"	4	–
Merecure	22	MERE	D	R	8°12' 50"	63°17' 25"	4	1
<i>Caura Lakes</i>								
Paso Acosta	23	PACO	D	R	7°21' 50"	65°11' 35"	3	1
Paramuto	24	PARA	D	R	7°33' 10"	65°00' 00"	4	1
Paramuto Forest	25	PFOR	–	R	7°33' 50"	65°00' 00"	4	–
Madera	26	MADE	D	R	7°33' 40"	65°00' 55"	3	1
Masaraca	27	MASA	D	R	7°36' 20"	64°53' 00"	4	–
Caño Masaraca	28	CMAS	–	R	7°37' 35"	64°51' 20"	4	–

* These sites were sampled during 1984 (inundation) and 1985 (isolation). The remaining sites were sampled during 1986 (inundation) and 1988 (isolation). During inundation, Lake Orsinera was sampled on 2 dates for analysis of major ion chemistry and on 14 dates for analysis of all other variables.

variation in turbidity across the lakes. For this reason, in contrast to the method used for oceanic embayments and large lakes (HAKANSON 1981), we placed the central point of the radials at the windward end of the lake shore rather than at the center of the lake.

Some lakes are channel-shaped, and will hereafter be referred to as channel lakes (ratio of length to width > 5). Other lakes are referred to as dish lakes. Channel lakes are formed and maintained by flowing waters, although flow may occur for only several

Table 2. Morphological characteristics of the sampling sites. All data are for the isolation phase except maximum depth and water flow, which pertain to inundation. Flow refers to the presence of surface currents during inundation; when currents were noticed, they usually ranged from 5–20 cm s⁻¹.

Site	Max. Length (km)	Max. Width (km)	L:W Ratio	Area (km ²)	Effect. Fetch (km)	Max. Depth (m)	Min. Depth (m)	Flow
<i>Orinoco lakes</i>								
CAST	2.7	1.7	1.6	2.57	1.09	8	1.7	
TEJA	2.3	0.6	3.7	0.67	0.67	7	–	
BART	2.7	1.0	2.6	1.55	0.80	7	1	
SAPO	2.2	0.2	11.0	0.47	–	14	–	yes
UYAP	7.0	1.3	5.5	15.26	–	31	15	yes
GUAI	2.3	0.9	2.7	1.23	1.01	13.7	–	
ESPE	2.8	0.2	14.5	0.42	–	10	–	yes
CLAR	1.7	0.1	26.5	0.19	–	11	–	yes
MALD	3.9	0.8	4.9	1.98	1.02	8	0.5	
PRAJ	0.7	0.6	1.2	0.33	–	7	0	
CARA	1.0	0.2	7.0	0.23	0.34	10	0.6	yes
CURI	0.4	0.1	3.9	0.03	0.13	8	0.5	
PBLA	0.5	0.2	2.5	0.09	0.41	4	0.5	
ORSI	0.6	0.3	2.2	0.11	0.44	6	1	
TINE	2.6	1.3	1.9	2.29	1.23	6	0.7	
TERE	0.6	0.1	5.6	0.05	0.19	5.5	2	yes
AGUI	0.9	0.1	6.5	0.10	0.23	6.5	2	yes
PAMP	0.3	0.1	2.2	0.02	0.15	4.5	1	
PIÑA	2.4	1.6	1.5	2.12	1.17	6	1	
PALM	1.3	0.8	1.6	0.78	0.65	7	–	
TIGR	1.1	0.5	2.1	0.40	0.68	5	–	
MERE	1.6	0.8	2.0	0.78	0.72	6	0.4	
<i>Caura lakes</i>								
PACO	0.4	0.3	1.5	0.05	0.21	5.5	0.85	
PARA	2.0	1.4	1.4	1.60	0.94	13.8	3.4	
PFOR*	–	–	–	–	–	8.3	–	
MADE	1.0	0.8	1.3	0.46	0.31	10.5	0.2	
MASA	3.7	1.1	3.3	2.85	1.25	13.3	–	
CMAS*	–	–	–	–	–	13.0	–	yes

* Flooded forest sites without discrete boundaries; morphometric variables do not apply.

months of the year. Dish lakes have gently sloping basins because they are formed in areas of sedimentation. Channel lakes are often deeper than dish lakes, and they have a lower ratio of surface area to volume. During inundation, some lakes receive most of their water from adjacent lakes rather than directly from the river; we define these lakes as serial lakes, and they can be either channel or dish lakes. Lakes Terecaya and Aguilera and Caño Uyape are serial channel lakes. Lake Pámpano (Fig. 1) is the only serial dish lake that was sampled. Serial lakes are most abundant in the more extensive floodplain areas located upriver.

The data are a composite of samples taken in different years (Table 1). Five lakes located in close proximity to each other (Tineo, Terecaya, Aguilera, Pámpano, and Piña; Fig. 1) were sampled at weekly or monthly intervals from June 1984—June 1985. We present time series for the chemistry of the five adjacent lakes and calculate mean values for chemical variables during inundation (July—November; 15 dates) and at the end of isolation (April—May; 2 dates) for comparison with other lakes. In addition to these lakes, we sampled 21 sites during inundation in 1986; most of the data presented here are means for 3—4 samplings performed at regular intervals between 31 July and 12 November. Additional isolation-phase data were collected in April 1988 from 12 lakes that had also been sampled during inundation in 1986. One lake (Tineo) was sampled at inundation and at isolation for three years; data for this site give an indication of inter-annual variation in lake chemistry.

Lakes were sampled in the center of the open-water area, where the water was usually deepest. We measured profiles of temperature (thermistor) and dissolved oxygen (polarographic electrode). Light penetration was estimated with a Secchi disk. Water was collected either as an integrated sample of the euphotic zone with a flexible plastic tube (1984—85) or from a depth of 0.5—1 m with a Van Dorn sampler (1986—88).

Samples were stored in a dark cooler and filtered within several hours of collection with tared Whatman GF/C glass-fiber filters (effective pore size, about 0.7 μm ; SHELDON 1972), which were then dried at 65 °C and reweighed to provide an estimate of total particulate material. Organic carbon on the filter (particulate C) was measured with a Carlo Erba elemental analyzer. For the isolation-phase samples, we estimated the concentration of organic particulate material as 2.5 times the concentration of particulate carbon (CAHILL et al. 1987); subtraction of this estimate from total particulate material yielded an estimate of the concentration of inorganic particulate material. Inundation-phase data are given as total particulates because particulate carbon was not determined in those samples. Additional GF/C filters containing particulate material were analyzed for particulate phosphorus by the method of SOLÓRZANO & SHARP (1980) and for chlorophyll-*a* by ethanol extraction, followed by spectrophotometric measurement with correction for phaeopigments (MARKER et al. 1980, NUSCH 1980).

Specific conductance (25 °C), pH, and total alkalinity (incremental titration: WETZEL & LIKENS 1979) were determined in the laboratory on unfiltered water, and all other solutes were measured in filtered samples (Whatman GF/C). Samples were analyzed for labile soluble components (pH, alkalinity, and inorganic nutrients) on the day after collection for most samples. However, for the 1988 isolation-phase samples, pH and alkalinity were measured after several months of storage. The sum of nitrate and nitrite (hereafter referred to as nitrate) was determined by cadmium-copper reduction of nitrate followed by colorimetric analysis of nitrite (WOOD et al. 1967); occasional analyses indicated that nitrite remained below the detection limit ($1 \mu\text{g L}^{-1}$). Ammonium was analyzed by the phenolhypochlorite technique (HARWOOD & KUHN 1970). Soluble reactive phosphorus (SRP) was determined by the ascorbic acid-molybdate method (MURPHY & RILEY 1962), and total soluble phosphorus (TSP) was analyzed by persulfate digestion, followed by analysis for soluble reactive phosphorus (VALDERRAMA 1981). Filtered samples were also analyzed for calcium, magnesium, sodium, and potassium by flame atomic absorption (after acidification to below pH 2 and addition of La_2O_3 and CsCl_2), and for chloride and sulfate by ion chromatography (unacidified subsamples). Silicon was determined in some filtered samples by a colorimetric molybdate analysis (ARMSTRONG & BUTLER 1962).

Collection and analysis of atmospheric deposition and local runoff

Samples of bulk atmospheric deposition were collected at biweekly intervals from collectors of the type described by LEWIS & GRANT (1978), located 10 m above ground in open areas. One collector was sampled during 1984–85 at a site several km upriver from Ciudad Bolívar; another one near the mouth of the Caura River was sampled during 1982–83. The collector surface was rinsed with a measured volume of deionized water when the sample was collected to wash any dry deposition that had accumulated on the surface into the sample. The samples were filtered and analyzed for major ions by methods similar to those used for analysis of lake samples. We sampled streams in the vicinity of Ciudad Bolívar for analysis of major ions on several occasions (see Results for sampling sites and dates).

Analysis of mixing systems using trilinear diagrams

Trilinear diagrams provide a graphical method for analyzing postulated mixing ratios using major ion chemistry as a tracer (PIPER 1953, MORRIS et al. 1983, HEM 1985). Ion concentrations (as meq L^{-1}) are expressed as a percentage of the total equivalents of cations or anions. The cation and anion data are plotted separately with triangular coordinates in the two lower fields; projection of these two points into the upper field yields a single point that represents the ionic composition of the sample. Where the major ions behave conservatively, mixtures formed from a combination of sources will plot within the polygon defined by the source chemistry in the upper field. Mixing proportions can be determined for mixtures of two or three sources from the position of the mixture relative to the sources, assuming that all major sources have been plotted.

Results

Chemical patterns during inundation

Concentrations of major cations during inundation were similar among lakes in close proximity to each other (Table 3), and were not highly variable over the course of the sampling period at a given site, as indicated by the coefficients of variation (means, 8–16%). Chloride and sulfate were more variable among lakes. Ion concentrations tend to increase in the downriver direction; specific conductance confirms this trend.

In the lakes of the Caura River floodplain, major ion concentrations were lower than those in lakes of the Orinoco (Table 3), reflecting the lower ionic strength of the Caura River (LEWIS et al. 1987). Ionic proportions also differ between the Orinoco and Caura lakes; on the basis of charge equivalents, Orinoco waters are dominated by calcium and bicarbonate, while those of the Caura are sodium-bicarbonate waters. Concentrations and proportions of ions for Lake Guaipure, which is located on the left bank of the Caura at its confluence with the Orinoco (site 6 in Fig. 1), indicate that this lake contained water from the Orinoco during inundation. For this reason, Lake Guaipure is listed with the Orinoco sites.

Table 3. Major ion concentrations (means with coefficients of variation in parentheses; mg L⁻¹), pH, and specific conductance (μS cm⁻¹; 25 °C) in floodplain lakes during inundation.

	Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	Cl ⁻	SO ₄ ²⁻	HCO ₃ ⁻	pH	Spec. Cond.
<i>Orinoco lakes</i>									
CAST	0.80 (14)	0.73 (14)	1.27 (7)	0.42 (9)	0.38 (29)	0.44 (9)	7.32 (18)	6.2	15.3 (11)
TEJA	0.80 (15)	0.75 (19)	1.33 (10)	0.47 (11)	0.37 (35)	0.47 (18)	7.52 (14)	6.1	15.8 (13)
BART	0.83 (17)	0.68 (6)	1.27 (7)	0.42 (6)	0.35 (10)	0.58 (11)	6.71 (7)	6.2	15.0 (9)
SAPO	0.79 (16)	0.63 (8)	1.40 (10)	0.45 (12)	0.29 (21)	0.73 (16)	6.56 (18)	6.1	15.6 (18)
UYAP	1.16 (37)	0.68 (13)	1.23 (12)	0.46 (11)	0.33 (26)	0.44 (39)	8.13 (20)	6.2	15.5 (19)
GUAI	0.87 (2)	0.65 (10)	1.24 (1)	0.42 (6)	0.98 (68)	0.44 (99)	5.86 (8)	6.3	14.3 (2)
ESPE	0.89 (12)	0.76 (5)	2.07 (8)	0.67 (7)	0.41 (17)	1.31 (9)	10.22 (10)	6.1	20.9 (6)
CLAR	0.94 (22)	0.72 (2)	2.07 (9)	0.63 (8)	0.37 (18)	1.43 (27)	9.76 (15)	6.2	21.3 (7)
MALD	0.94 (9)	0.90 (9)	2.28 (5)	0.76 (6)	0.50 (17)	1.13 (30)	11.59 (5)	6.3	23.9 (6)
PRAJ	1.24 (28)	0.97 (20)	2.41 (20)	0.73 (10)	0.72 (40)	0.89 (27)	12.20 (22)	6.2	24.0 (14)
CARA	1.08 (14)	0.97 (3)	2.96 (10)	0.93 (9)	0.59 (17)	1.63 (10)	14.02 (15)	6.2	29.8 (9)
CURI	1.24 (8)	1.30 (4)	2.78 (12)	0.98 (11)	0.88 (30)	1.42 (15)	14.94 (15)	6.1	30.1 (9)
ORSI	1.08 (6)	1.16 (23)	3.24 (10)	0.96 (9)	—	—	—	—	—
TINE	1.18 (14)	0.77 (17)	3.00 (5)	0.73 (10)	0.69 (42)	1.90 (25)	11.32 (17)	6.5	31.3 (9)
TERE	1.13 (14)	0.82 (20)	3.03 (5)	0.72 (6)	0.68 (51)	2.02 (29)	11.77 (16)	6.4	31.1 (8)
AGUI	1.14 (14)	0.82 (12)	3.01 (5)	0.72 (6)	0.68 (44)	1.87 (19)	11.47 (19)	6.5	31.0 (8)
PAMP	1.22 (28)	0.84 (21)	3.05 (10)	0.74 (15)	0.75 (75)	2.08 (43)	11.63 (21)	6.5	31.6 (17)
PINA	1.11 (8)	0.80 (6)	2.98 (7)	0.71 (4)	0.64 (36)	2.16 (21)	11.26 (19)	6.7	29.6 (9)
PALM	1.18 (23)	0.92 (14)	2.44 (9)	0.76 (9)	0.63 (36)	1.18 (29)	12.20 (19)	6.1	27.7 (5)
TIGR	0.94 (10)	0.89 (14)	2.54 (13)	0.80 (13)	0.45 (16)	1.09 (24)	12.65 (22)	6.4	24.8 (12)
MERE	1.08 (20)	0.99 (15)	2.57 (11)	0.85 (12)	0.66 (28)	1.01 (51)	13.57 (19)	6.2	25.9 (9)
Means	1.03 (16)	0.84 (12)	2.29 (9)	0.68 (9)	0.57 (33)	1.21 (28)	10.53 (16)	6.2	23.7 (10)
<i>Caura lakes</i>									
PACO	0.90 (4)	0.50 (13)	0.41 (21)	0.19 (13)	0.60 (79)	0.03 (79)	4.31 (12)	5.9	9.8 (9)
PARA	0.95 (10)	0.61 (5)	0.54 (5)	0.23 (4)	0.22 (2)	0.14 (126)	4.43 (10)	6.2	9.9 (10)
PFOR	0.96 (4)	0.60 (7)	0.53 (6)	0.23 (4)	0.27 (16)	0.05 (43)	4.09 (10)	6.1	10.0 (8)
MADE	0.98 (3)	0.61 (8)	0.53 (4)	0.23 (6)	0.30 (39)	0.04 (124)	4.12 (9)	6.2	10.3 (10)
MASA	0.80 (44)	0.62 (4)	0.70 (20)	0.27 (11)	0.25 (5)	0.17 (67)	4.97 (11)	6.1	11.4 (7)
CMAS	0.96 (9)	0.62 (5)	0.64 (12)	0.26 (9)	0.24 (3)	0.13 (57)	4.33 (4)	5.9	11.0 (6)
Means	0.92 (12)	0.59 (7)	0.56 (11)	0.23 (8)	0.31 (24)	0.09 (83)	4.38 (9)	6.0	10.4 (8)

All lakes were below saturation for dissolved oxygen during inundation (oxygen solubility at 26–29 °C: 8.1–7.7 mg L⁻¹) (Table 4). Although thermal stratification was common in the lakes during inundation, none of the lakes was consistently anoxic in the hypolimnion during inundation. Thermal and dissolved oxygen profiles varied considerably within and among sites during inundation, and appeared to be strongly influenced by the variable patterns of riverine through-flow in the lakes (HAMILTON & LEWIS 1987, HAMILTON et al. 1990). An increase in dissolved oxygen concentration with depth was observed on two dates in Lake Guaipure, and has been noted in other lakes on a few occasions; these anomalous oxygen profiles might result from advection driven by riverine inflows, or from differential heating of the lakes.

Table 4. Dissolved oxygen (0.5 m below surface and 0.5 m above bottom; concentrations in $\text{mg} \cdot \text{L}^{-1}$), total particulates ($\text{mg} \cdot \text{L}^{-1}$), Secchi depth (m), chlorophyll-a ($\mu\text{g} \cdot \text{l}^{-1}$), and nutrients ($\mu\text{g} \cdot \text{l}^{-1}$) in floodplain lakes during inundation (means with coefficients of variation in parentheses). SRP – soluble reactive phosphorus; TSP – total soluble phosphorus.

	Dissolved Oxygen		Total Partic.	Secchi	Chl-a	NO_3^-	NH_4^+	SRP	TSP	Partic. P
	Surface	Bottom								
<i>Orinoco lakes</i>										
CAST	5.1 (5)	3.4 (27)	4.2 (4)	1.3 (14)	8.0 (26)	6 (56)	20 (25)	6 (27)	13 (9)	11 (11)
TEJA	4.1 (17)	3.0 (16)	3.5 (37)	1.3 (13)	9.6 (48)	9 (47)	17 (6)	8 (30)	15 (22)	13 (23)
BART	4.5 (11)	2.5 (29)	4.4 (26)	1.1 (12)	7.9 (17)	21 (47)	16 (21)	11 (43)	18 (31)	9 (5)
SAPO	3.5 (24)	2.2 (94)	16.9 (13)	0.4 (10)	5.6 (93)	45 (22)	20 (16)	10 (21)	21 (40)	18 (50)
UYAP	4.9 (24)	–	8.8 (43)	0.9 (39)	17.7 (63)	24 (47)	14 (19)	7 (29)	16 (37)	12 (24)
GUAI	2.9 (12)	3.6 (4)	2.1 (30)	1.4 (7)	7.5 (0)	7 (53)	14 (13)	7 (7)	14 (9)	13 (5)
ESPE	4.1 (10)	3.4 (7)	13.5 (25)	0.4 (20)	2.1 (39)	57 (33)	22 (15)	12 (11)	19 (13)	16 (17)
CLAR	4.9 (9)	3.8 (22)	16.3 (28)	0.4 (20)	2.4 (44)	60 (34)	13 (13)	11 (22)	17 (18)	19 (17)
MALD	5.2 (12)	2.9 (36)	6.9 (25)	1.0 (10)	17.2 (44)	12 (134)	14 (30)	11 (12)	18 (24)	21 (25)
PRAJ	3.1 (44)	1.6 (97)	6.3 (26)	0.9 (14)	6.1 (35)	12 (108)	14 (29)	8 (37)	18 (25)	16 (27)
CARA	3.4 (24)	2.9 (15)	19.8 (23)	0.5 (27)	2.2 (27)	50 (37)	15 (23)	16 (13)	22 (11)	23 (33)
CURI	3.8 (55)	2.5 (59)	5.6 (50)	1.2 (40)	5.7 (51)	9 (105)	13 (15)	8 (29)	17 (13)	13 (34)
ORSI	–	–	13.5 (106)	–	–	4 (143)	70 (41)	10 (72)	22 (65)	29 (37)
TINE	6.5 (13)	3.9 (29)	14.9 (37)	0.6 (36)	–	13 (144)	70 (36)	7 (58)	17 (36)	28 (16)
TERE	3.9 (10)	3.6 (16)	16.0 (23)	0.5 (24)	–	19 (62)	78 (37)	7 (45)	19 (28)	26 (17)
AGUI	4.4 (21)	3.5 (16)	16.8 (31)	0.5 (20)	–	22 (62)	72 (45)	7 (46)	19 (31)	29 (22)
PAMP	4.0 (26)	2.9 (38)	14.7 (25)	0.6 (26)	–	16 (72)	61 (30)	6 (49)	19 (21)	33 (33)
PINA	6.1 (13)	3.3 (45)	12.3 (25)	0.7 (28)	–	6 (95)	70 (41)	7 (45)	20 (47)	26 (16)
PALM	3.0 (13)	1.9 (35)	6.9 (13)	0.8 (30)	19.3 (97)	13 (74)	16 (10)	9 (50)	17 (30)	22 (29)
TIGR	5.3 (8)	2.7 (52)	10.8 (13)	0.7 (17)	12.2 (60)	22 (95)	12 (16)	11 (24)	18 (20)	20 (6)
MERE	4.4 (15)	1.2 (108)	8.5 (46)	0.9 (22)	36.0 (60)	6 (66)	13 (20)	10 (37)	19 (29)	34 (29)
Means	4.4 (18)	2.9 (39)	10.6 (31)	0.8 (21)	10.6 (47)	21 (73)	31 (24)	9 (34)	18 (27)	20 (23)
<i>Caura lakes</i>										
PACO	4.1 (20)	1.6 (72)	9.2 (105)	1.7 (14)	37.0 (127)	21 (89)	16 (43)	4 (89)	12 (46)	22 (97)
PARA	6.2 (11)	3.5 (64)	1.9 (28)	1.6 (15)	6.4 (96)	49 (20)	13 (19)	2 (64)	8 (31)	7 (28)
PFOR	6.0 (12)	2.1 (92)	1.5 (37)	2.0 (18)	8.8 (50)	34 (57)	14 (31)	1 (81)	8 (35)	5 (17)
MADE	6.3 (5)	5.6 (14)	1.6 (37)	1.8 (18)	3.8 (55)	59 (3)	14 (28)	1 (72)	7 (40)	6 (2)
MASA	5.8 (16)	3.1 (36)	2.0 (50)	1.8 (12)	5.9 (59)	39 (20)	13 (22)	3 (20)	9 (14)	8 (17)
CMAS	5.2 (7)	4.0 (–)	1.4 (33)	2.1 (7)	5.9 (69)	48 (10)	10 (14)	2 (37)	9 (10)	6 (33)
Means	5.6 (12)	3.3 (56)	2.9 (48)	1.8 (14)	11.3 (76)	42 (33)	13 (26)	2 (60)	9 (29)	9 (33)

In contrast to the major ions, concentrations of particulates and macronutrients were variable during inundation (Table 4), even among adjacent lakes, and variation over time at a given site was often large. In several cases (e.g., lakes Maldonado, Merecure, and Paso Acosta), concentrations of chlorophyll-a were particularly variable (Table 4). This variation was also evident from observations of water color in the field. The concentration of ammonium was higher in 1984 than in 1986 (Table 4).

The Caura lakes were generally lower in total particulate material, higher in nitrate and lower in all forms of phosphorus than the Orinoco lakes (Table 4). The exceptionally high mean concentration of chlorophyll-a in Lake Paso Acosta resulted from a bloom observed on 27 September 1986, when the con-

centration of chlorophyll-a was $103 \mu\text{g L}^{-1}$. This lake also differed from the other Caura lakes because of its higher concentrations of particulate material and phosphorus and lower concentration of nitrate.

Chemical divergence of lakes during isolation

Chemical data for the five lakes sampled throughout an annual cycle of inundation and isolation during 1984–85 illustrate the divergence of lake chemistry that occurs after riverine through-flow ceases. These five lakes became interconnected during inundation (Fig. 1), with substantial flow entering from the river and passing between lakes through narrow tie channels. The chemistry of these lakes rapidly converged during inundation as river water flushed their basins. The overwhelming effect of flushing on lake chemistry was quantitatively demonstrated for one of the largest lakes (Tineo) by HAMILTON & LEWIS (1987), through the use of a mass-balance model. Time series of selected chemical variables for the five lakes will be presented here for the period of chemical divergence, which began when riverine through-flow tapered off in November and continued during the ensuing isolation phase.

Data on thermal and dissolved oxygen profiles for one of the dish lakes (Tineo) and one of the channel lakes (Aguilera) were presented in HAMILTON *et al.* (1990), and are generally representative of the five lakes. Thermal stratification and a lower concentration of oxygen near the bottom were usually observed during isolation in the two channel lakes (Terecaya and Aguilera), while the other three lakes were usually isothermal and evidently mixed more regularly. Surface waters were commonly above saturation for dissolved oxygen during the day in lakes Tineo, Aguilera, and Pámpano. Water levels of the five lakes decreased steadily by evaporation after they became isolated from each other (HAMILTON & LEWIS 1987), falling 0.4–0.6 m between 28 January and 17 June 1985.

Time series of major ion concentrations in the five lakes over the course of the isolation phase are shown in Fig. 3. At the beginning of this period (4 November 1984), all of the lakes were still interconnected, although Lake Pámpano was no longer receiving water from adjacent lakes, and ion concentrations in the lakes were similar. The first lake to diverge from the rest in ion chemistry was Lake Pámpano, which was the first to become isolated. Lake Pámpano decreased in total ion concentration, primarily because of decreased concentrations of calcium, magnesium, potassium, and bicarbonate; the sulfate concentration increased. Lake Piña was the next to diverge; it showed a large increase in chloride and potassium concentrations in late November and December. During isolation, pH in the five lakes was variable but generally higher than it was during inundation, occasionally exceeding 8.5 in several lakes. By the end of the isolation phase, the five lakes varied considerably in ion concentrations and proportions.

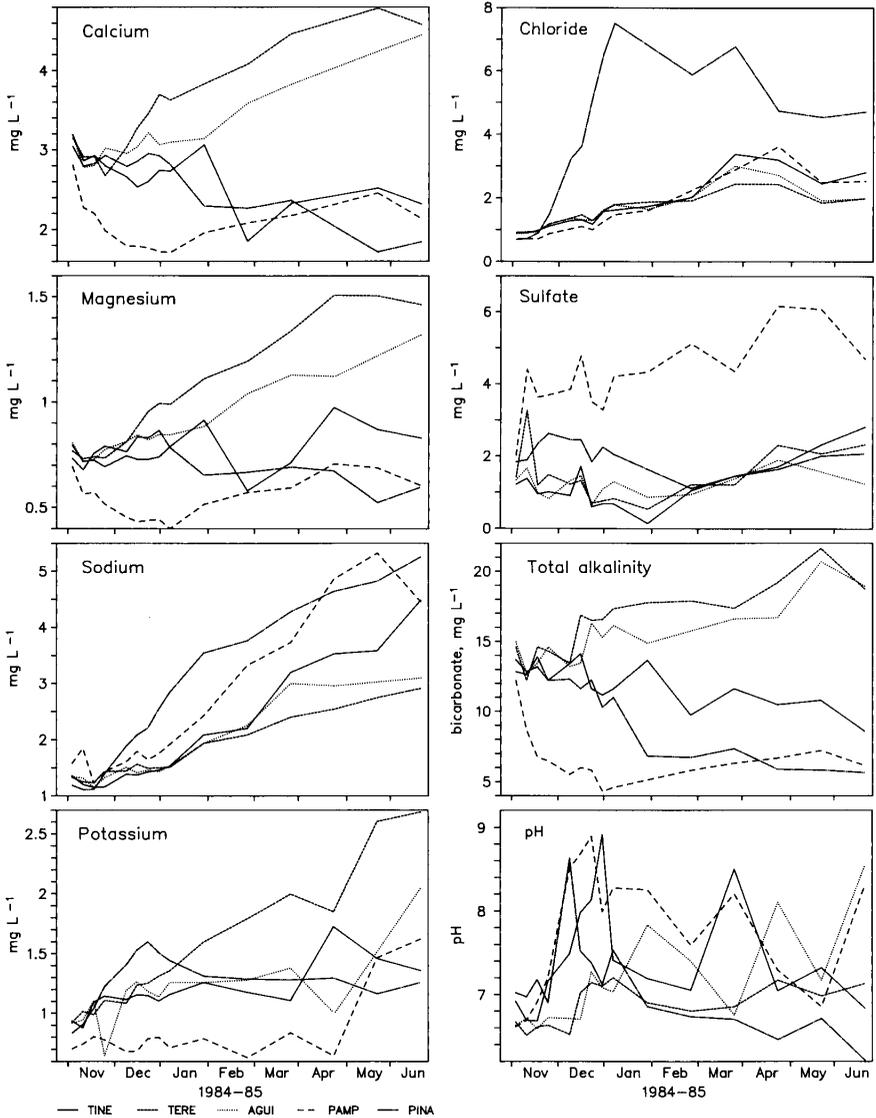


Fig. 3. Major ion concentrations and pH in five adjacent lakes during the period of chemical divergence (drainage and isolation phases). Full names of lakes are given in Table 1.

The lakes began the isolation phase with similar concentrations of inorganic nutrients, but subsequently diverged (Fig. 4). The peak in SRP concentration in all five lakes on 11 November 1984 occurred immediately after a very large rainfall, and thus probably resulted from runoff. The larger peaks in SRP and nitrate during February–April are less likely to have resulted from

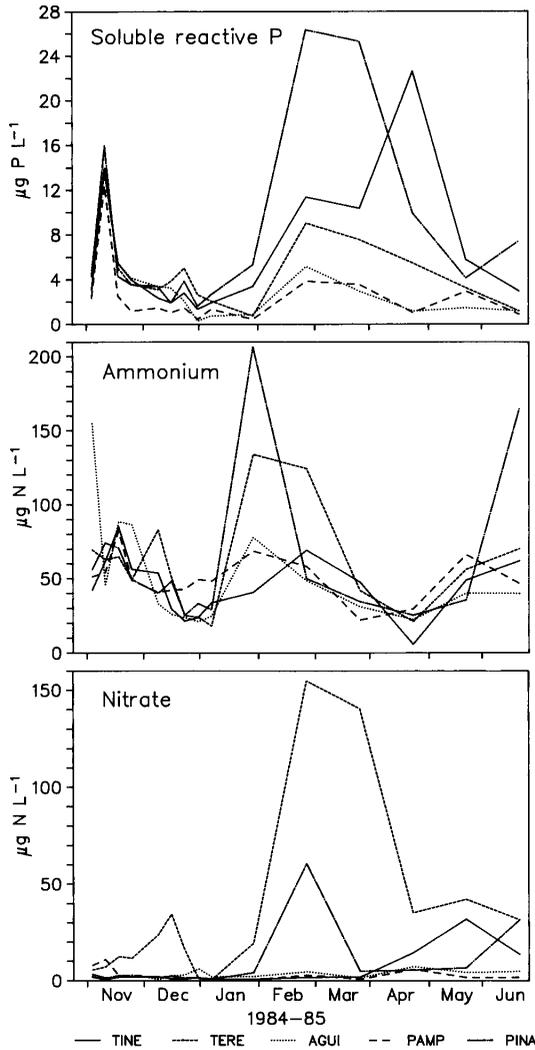


Fig. 4. Concentrations of soluble reactive phosphorus, ammonium and nitrate in five adjacent lakes during the period of chemical divergence (drainage and isolation phases). Full names of lakes are given in Table 1.

runoff, however, because rainfall was very low during this period. With regard to surface-water connections, all of the lakes were isolated from each other and from the river after early January. Vertical profiles of temperature and dissolved oxygen, which were measured three times per month during this period, do not provide evidence for an unusual mixing event corresponding with the dates of increase. Therefore, the increases are difficult to explain, but they

do suggest that synoptic information on nutrient concentrations in these lakes during isolation may not be obtainable from single sampling dates.

Concentrations of inorganic particulate material and particulate carbon in the five lakes also diverged during isolation (Fig. 5). Resuspension of sediments increased the concentration of inorganic particulates in lakes Tineo and Piña during late isolation (Table 2). However, the initial increase in inorganic particulates in Lake Piña during January resulted not from resuspension but from the entry of turbid water from neighboring lakes to the east; sediment resuspension in Piña was probably not important until May and June. The data on inorganic particulates do not show significant sediment resuspension in the other three lakes.

During algal blooms, particulate carbon can be comprised largely of phytoplankton biomass in these lakes (HAMILTON & LEWIS 1987). The concentration of particulate carbon increased first in Lake Pámpano, and remained considerably higher in this lake than in the others throughout isolation; this

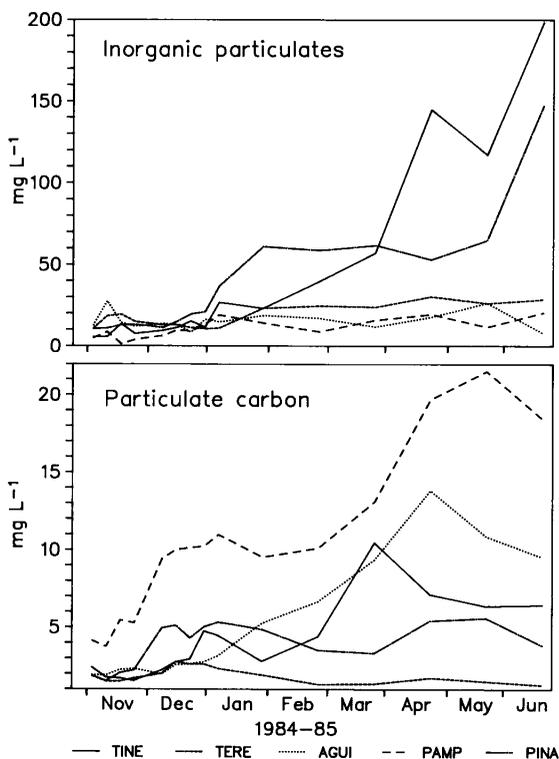


Fig. 5. Concentrations of inorganic particulate material and particulate carbon in five adjacent lakes during the period of chemical divergence (drainage and isolation phases). Full names of lakes are given in Table 1.

Table 6. Inorganic particulate material and particulate carbon concentrations ($\text{mg} \cdot \text{L}^{-1}$), Secchi depth (m), nitrogen ($\mu\text{g} \cdot \text{N} \cdot \text{L}^{-1}$) and phosphorus ($\mu\text{g} \cdot \text{P} \cdot \text{L}^{-1}$) in floodplain lakes during late isolation (April–May).

	Inorg. Partic.	Partic. Carbon	Secchi	NO_3^-	NH_4^+	SRP	TSP	Partic. P
<i>Orinoco lakes</i>								
CAST	63	1.4	0.10	–	–	–	140	76
TEJA	–	–	–	–	–	–	–	–
BART	415	8.0	0.05	–	–	–	155	299
SAPO	–	–	–	–	–	–	–	–
UYAP	–	–	–	–	–	–	–	–
GUAI	–	–	–	–	–	–	–	–
ESPE	–	–	–	–	–	–	–	–
CLAR	–	–	–	–	–	–	–	–
MALD	441	19	0.04	–	–	–	85	336
PRAJ	–	–	–	–	–	–	–	–
CARA	50	2.5	–	–	–	–	36	47
CURI	19	3.3	0.40	–	–	–	13	5
PBLA	272	10	–	–	–	–	–	–
ORSI	117	6.5	–	21	131	18	64	60
TINE	131	6.8	0.07	23	27	14	40	167
TERE	28	1.6	0.25	39	39	4	22	67
AGUI	22	12	0.20	4	31	1	17	77
PAMP	16	21	0.20	6	48	2	22	191
PIÑA	59	5.5	0.15	6	30	7	27	97
PALM	230	4.4	0.05	–	–	–	202	230
TIGR	–	–	–	–	–	–	–	–
MERE	375	11	0.05	–	–	–	–	239
<i>Caura lakes</i>								
PACO	25	4.3	0.40	–	–	–	14	2
PARA	1	6.2	0.60	–	–	–	20	19
PFOR	–	–	–	–	–	–	–	–
MADE	92	21	0.10	–	–	–	45	263
MASA	–	–	–	–	–	–	–	–
CMAS	–	–	–	–	–	–	–	–

The results of the isolation-phase survey are presented in Tables 5 (major ions and silica) and 6 (particulates and nutrients). We have included means for the April–May data from the five lakes sampled in 1985 for comparison. Fewer lakes were sampled during isolation than during inundation, and labile nutrients were not determined in 1988. Thermal and dissolved oxygen profiles indicated that the lakes were generally well-mixed during isolation, as expected given their shallow depths at this time (Table 2). As with the five lakes sampled during 1985, concentrations and proportions of major ions were variable among lakes (Table 5). Silica also varied in concentration. The highest ionic strength was found in Lake Curita, which by the time of sampling was reduced

to a small, shallow pool surrounded by an extensive mud flat. Many lakes were highly turbid because of sediment resuspension.

Interannual variation in lake chemistry

We have sampled Lake Tineo during inundation and isolation in three different years (Table 7). There was less interannual variation in chemistry during inundation than during isolation. Major ions varied in concentration among years, but ionic proportions were less variable. Nutrient concentrations varied substantially between the two years for which data are available. Although significant interannual variation is apparent, consistent seasonal differences are clearly visible among years for some variables. In particular, the concentration of total particulates was always an order of magnitude higher at isolation than at inundation, and the dominant cation consistently changed from calcium at inundation to sodium at isolation.

Chemistry of bulk atmospheric deposition and local runoff

Volume-weighted mean concentrations of major ions in atmospheric deposition collected at Ciudad Bolívar and at the mouth of the Caura River are

Table 7. Interannual variation in chemistry of Lake Tineo. Isolation-phase samples are from Apr–May and inundation-phase samples are from Jul–Nov. Part. = total particulates ($\text{mg} \cdot \text{L}^{-1}$); cond. = specific conductance ($\mu\text{S cm}^{-1}$; 25°C); CV = coefficient of variation, %. Major ion concentrations are in mg L^{-1} and nutrient concentrations are in $\mu\text{g} \cdot \text{L}^{-1}$.

	Isolation				Inundation			
	1984	1985	1988	Mean (CV)	1984	1986	1988	Mean (CV)
Dates	3	2	1		15	4	2	
Ca ²⁺	2.45	2.52	1.52	2.2 (23)	3.00	2.77	2.75	2.8 (4)
Mg ²⁺	0.81	0.92	0.50	0.7 (29)	0.73	0.83	0.80	0.8 (0)
Na ⁺	3.47	3.56	1.76	2.9 (28)	1.18	1.09	1.35	1.2 (8)
K ⁺	1.03	1.59	1.33	1.3 (15)	0.77	0.91	1.00	0.9 (11)
SO ₄ ⁻²	3.57	2.02	2.40	2.7 (26)	1.90	1.56	1.61	1.7 (6)
Cl ⁻	4.62	2.82	2.21	3.2 (31)	0.69	0.49	1.02	0.7 (29)
HCO ₃ ⁻	10.5	10.6	7.3	9.4 (16)	11.3	13.1	10.5	11.6 (9)
pH	6.7	7.2	5.7	6.1 (-)	6.6	6.3	6.6	6.5 (-)
Cond.	37.9	33.0	27.3	32.7 (13)	29.1	26.7	28.5	28.1 (4)
NO ₃ ⁻	100	23	-	61 (63)	13	12	-	12 (4)
NH ₄ ⁺	65	27	-	46 (41)	70	15	25	37 (65)
SRP	36	6	-	21 (71)	7	10	-	9 (18)
TSP	-	36	49	43 (15)	17	19	-	18 (6)
Part. P	138	97	221	152 (34)	28	18	-	23 (22)
Part.	175	148	359	227 (41)	14.9	10.3	23.6	16 (37)
Part. C	5.3	6.8	8.8	6.9 (20)	1.6	1.3	1.0	1.3 (19)

Table 8. Volume-weighted mean concentrations of major ions in bulk atmospheric deposition collected near Ciudad Bolívar and near the mouth of the Caura River. Units are $\text{mg} \cdot \text{L}^{-1}$.

	Ciudad Bolívar		Caura
	Annual:	Dry Season:	20-mo. Mean:
	10 May 83 – 16 May 85	Jan – Jun 1984 and 1985	21 Jun 82 – 29 Feb 84
Ca^{2+}	2.87	1.13	0.14
Mg^{2+}	0.74	0.49	0.03
Na^+	6.33	3.58	3.09
K^+	1.38	1.38	0.16
Cl^-	15.37	7.88	4.90
SO_4^{2-}	5.56	2.81	0.75
HCO_3^-	0.20	1.04	0

Table 9. Concentrations of major ions in local streams in the vicinity of Ciudad Bolívar. Bicarbonate was not determined. Units are $\text{mg} \cdot \text{l}^{-1}$.

Stream	Ca^{2+}	Mg^{2+}	Na^+	K^+	Cl^-	SO_4^{2-}
Quebrada El Chorro ¹	2.42	2.89	21.4	11.3	–	–
Morichal Aracaicú ²	0.21	0.21	1.38	0.65	2.08	1.38
Río Carapa ³	0.2	0.3	3.2	1.1	5.19	0.36
Morichal Pardillal ³	0.2	0.3	3.0	1.5	5.20	0.36
Río Carmona ³	0.2	0.3	3.1	0.9	5.57	0.27

¹ Ephemeral first-order stream flowing into Lake Piña; sampled 23 Nov 1984.

² Perennial first-order stream flowing into Lake Maldonado; sampled 16 Jul and 16 Oct 1986.

³ Perennial second-order streams flowing into the floodplain to the east of Lake Piña; sampled 13 Oct (Carapa) or 22 Oct 1988.

summarized in Table 8. At both sites, sodium and chloride are the dominant ions in atmospheric deposition throughout the year. Ion concentrations are lower in atmospheric deposition at the Caura site (LEWIS et al. 1987). Samples collected from several local streams indicate that local runoff is also dominated by sodium and chloride, and resembles atmospheric deposition in ionic proportions (Table 9). Atmospheric deposition and stream runoff differ substantially in ion chemistry from the Orinoco River, in which calcium and bicarbonate ions dominate.

Discussion

Patterns in lake chemistry during inundation

During inundation, the hydrologic dominance of the river results in a tendency toward uniformity in major ion chemistry among lakes. Concentrations of major ions were similar in adjacent lakes of variable morphometry and

water residence times (as indicated by presence or absence of currents), suggesting that the major ions were not strongly affected by processes within the lakes at that time. The observed increase in ion concentrations in lakes in the downriver direction could therefore reflect differences in the chemistry of river water entering the lakes or, alternatively, it could reflect a gradient in the proportions of water from different sources in the floodplain lakes. In addition to the river, potentially significant water sources include local rain and runoff. To understand chemical patterns in the lakes during inundation, we must first address this question of potential water sources.

A downriver increase in the ionic strength of river water along the right bank could result from progressively greater lateral mixing of water of higher ionic strength from the left-bank tributaries (Meta and Apure rivers: Fig. 1) with water along the right bank. MEADE *et al.* (1983) presented data on suspended particulates to show that water from the Meta and Apure can travel in the Orinoco main channel to below the Caura River without full lateral mixing. LEWIS & SAUNDERS (1984) showed cross-section heterogeneity in major ion chemistry as far downriver as Ciudad Bolívar.

An alternative explanation is that the gradient is caused by a decreasing influence of rainfall (and hence local runoff) in the downriver direction. Mean annual precipitation decreases from $> 1600 \text{ mm y}^{-1}$ in the upriver section to ca. 900 mm y^{-1} in the downriver section (MARNR 1983).

The disparity in major ion chemistry between local water (atmospheric deposition and stream runoff) and Orinoco River water provides an opportunity to use major ion concentrations as hydrologic tracers of these water types. Discharge-weighted means for major ions in the Orinoco above the Apure and in the Apure and Caura rivers were calculated for the high-water period (August–October 1982–85, from LEWIS *et al.* 1987, LEWIS & SAUNDERS 1989, and SAUNDERS & LEWIS 1989). A floodplain lake will receive water from the three river components plus an unknown amount of local water. We have plotted the ionic composition of the three river components and of atmospheric deposition and local runoff (potential sources) together with that of the floodplain lakes (mixtures) in Fig. 6.

All of the lakes plot close to the triangle defined by the three riverine sources and do not show a detectable influence of local water on their ionic proportions. We conclude that the downriver increase probably results from delayed mixing of tributary influents across the main channel, which in turn causes a downriver gradient in the ionic composition of river water entering lakes along the right bank. A similar gradient probably exists for particulate material and nutrients in water entering the lakes; the Apure and Meta rivers are more turbid and richer in inorganic nitrogen and phosphorus than water of the upper Orinoco (SAUNDERS & LEWIS 1989, LEWIS & SAUNDERS 1989).

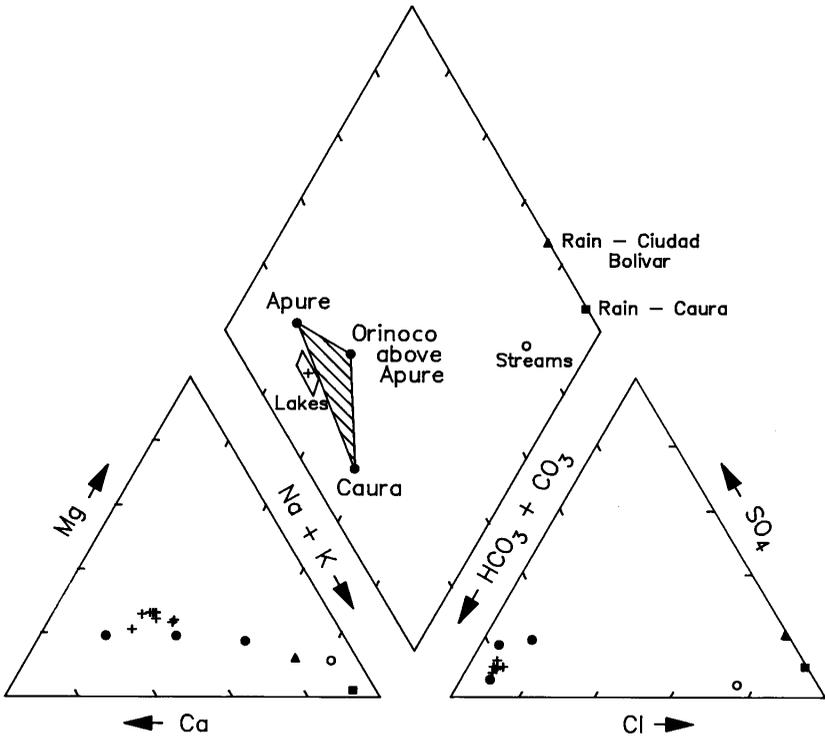


Fig. 6. Trilinear diagram comparing the ionic proportions in floodplain lakes at inundation with those of potential sources of water.

Variation among lakes in particulate material and nutrients (N and P) during inundation is related to differences in their morphology. Scatterplots of these variables separate Caura lakes from Orinoco lakes, and Orinoco dish lakes from Orinoco channel lakes (Fig. 7). Serial channel lakes plot close to dish lakes because they receive water from dish lakes upstream in the flow path across the floodplain, and thus reflect the chemistry of dish lakes.

Flow paths across the floodplain and water residence times in individual basins appear to determine the degree that floodplain processes cause chemical changes in river water. Concentrations of labile nutrients and particulates in channel lakes during inundation are similar to those of the source water from the river. Dish lakes show the greatest deviation from the source water. The Orinoco dish lakes show pronounced sedimentation of particulate material, loss of nitrate, and growth of phytoplankton. Similar changes occur in channel lakes, but only after the rate of through-flow declines and the lakes become isolated (HAMILTON et al. 1990).

Lower amounts of particulate material and of soluble and particulate phosphorus in the Caura River are reflected by the chemistry of the Caura lakes, al-

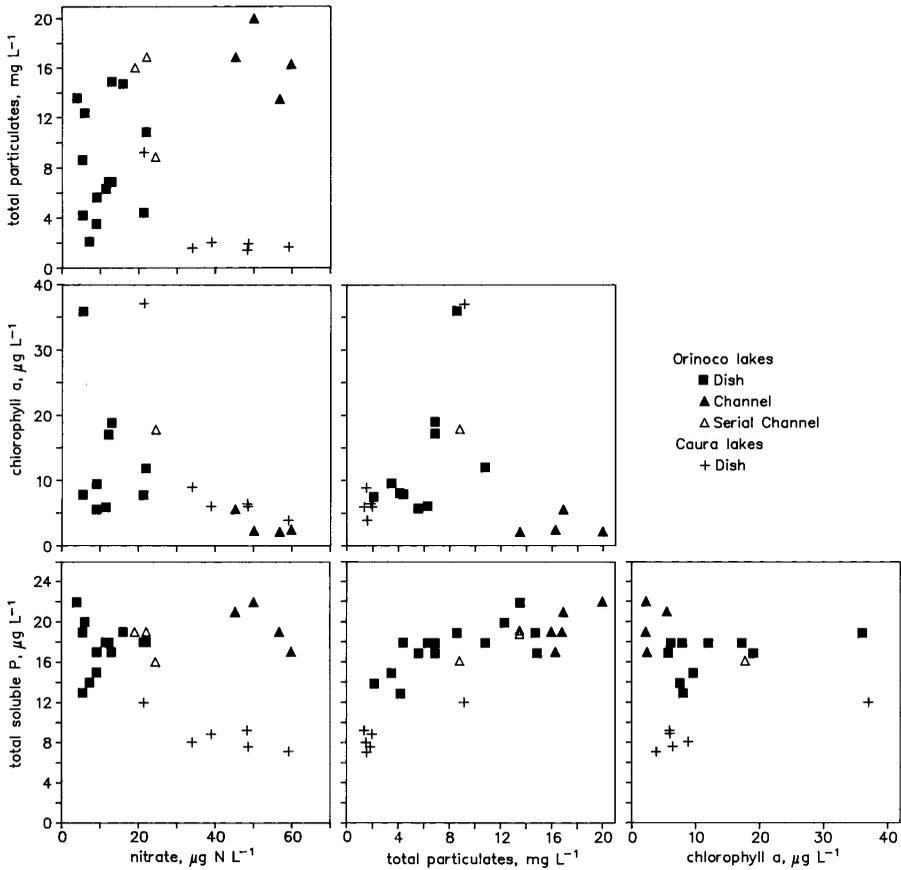


Fig. 7. Scatterplots showing the relationships between nitrate, total soluble phosphorus, chlorophyll-a, and total particulate material in floodplain lakes during inundation.

though the river supplies appreciable nitrate (LEWIS 1986). The concentration of nitrate remained relatively high during inundation in the Caura lakes, which are dish lakes, in contrast to the nitrate depletion observed in Orinoco dish lakes. The chlorophyll-a concentration remained low in the Caura lakes. Lake Paso Acosta, in contrast to other Caura lakes, had higher concentrations of inorganic turbidity and phosphorus and greater algal growth, probably due to the influence of a perennial stream that flows into the floodplain near this small lake.

The persistence of nitrate and lower accumulation of phytoplankton biomass in the Caura lakes is surprising, particularly because light transmission in these lakes was higher than in the Orinoco lakes (Table 4), and suggests that low concentrations of phosphorus, rather than nitrogen, may limit autotrophic production in the Caura lakes. Caura lakes lack floating vascular plants

such as *Paspalum repens* and *Eichornia crassipes*, which are abundant throughout the Orinoco floodplain. Phosphorus availability may limit the growth of aquatic vascular plants as well as algae on the Caura floodplain. Comparable nutrient limitation may exist in the floodplain of the Rio Negro (SCHMIDT 1972, GOULDING et al. 1988) in Brazil.

If atmospheric exchange is the principal source of oxygen to the lakes (MELACK & FISHER 1983), oxygen depletion in bottom waters should be directly related to the depth of the water column and inversely related to the effective fetch of the lake. The vertical gradient in dissolved oxygen concentration during inundation (Table 4) provides a measure of depletion of dissolved oxygen. Through-flow controls the concentration of dissolved oxygen in channel lakes. Among dish lakes, linear regression analyses indicate that depletion of dissolved oxygen is not significantly related to fetch or to maximum depth, although a weak but significant relation is found between the oxygen gradient and the ratio of effective fetch to maximum depth ($EF:Z_{max}$; Fig. 8). The substantial scatter around the regression line in Fig. 8 is probably explained by variability in water residence times among dish lakes. The dissolved oxygen gradient in floodplain lakes is thus difficult to predict from morphometric measurements made from maps unless information on lake depths is also available.

Causes of chemical divergence during isolation

Although evaporation is responsible for much of the observed increase in ion concentrations in the lakes (HAMILTON & LEWIS 1987), evapoconcentration

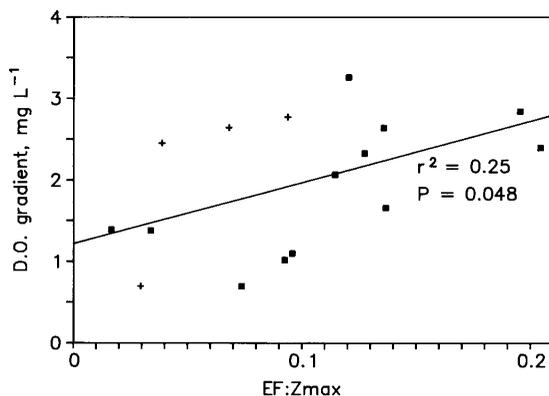


Fig. 8. Relationship between lake morphometry and the gradient in dissolved oxygen (D.O.) concentration between the surface (0.5-m depth) and the bottom (ca. 0.5 m above bottom), for dish lakes during the inundation phase (squares = Orinoco lakes, pluses = Caura lakes). $EF:Z_{max}$ = ratio of effective fetch (km) to maximum depth (m; depth at the center of the lake during its highest water level). The regression equation is

$$Y = 7.48X + 1.22.$$

of lake waters should lead to congruent increases in ion concentrations, at least for those ions which are most conservative. Among the five lakes in Fig. 3, the observed increases in ion concentrations are incongruent, which suggests that the changes could be caused at least partly by influx of water with different ionic proportions and higher concentrations of certain ions.

The continual contraction of the lakes during isolation increases their ratio of surface area to volume, thereby increasing the relative contribution of a rainfall or groundwater source. Although streams or shoreline seeps were found only along Lake Piña, local waters could have entered the other four lakes during isolation by rainfall directly on the lake surface, by overland runoff during storms, or by groundwater seepage. A water budget for one of the lakes (Tineo) for this period (1984–85) showed that rain falling on the lake surface was a small proportion of the total input of water to the lake during inundation, but was significant over the course of isolation (HAMILTON & LEWIS 1987).

Changes in major ion chemistry in the lakes during isolation reflect hydrological processes, but the relative importance of these processes varies among the five lakes (Fig. 9). Lake Pámpano showed the greatest change in ionic proportions, followed by Lake Piña. Both of these lakes turned sharply in the direction of change after 6 January. Lake Tineo changed less and its change was unidirectional. Lakes Terecaya and Aguilera, which are small channel lakes (Fig. 1), changed the least over the course of isolation. The ionic proportions of atmospheric deposition and of streams are also plotted in Fig. 9. Rainfall, as indicated by the size of the circles, was much greater in November and December than in the following months. Most of the November rain fell in a single storm on 11 November. Upon our arrival at the lakes within hours of this storm, it was obvious that much more rain fell at the lakes than at our collector (14 km upriver) or at Ciudad Bolívar (9 km away); the circle in Fig. 9 is thus a minimum estimate for November. The change in lake chemistry toward that of the rainfall indicates that rain contributed significantly to the volume of water in the lakes. In the two channel lakes (Terecaya and Aguilera), the sudden change was followed by reversion to the original proportions by the next week; these lakes were still being flushed with water that flowed out of Lake Tineo.

Variation in the proportions of local water in the three dish lakes during isolation may be explained by differences in morphology as well as in their relative positions on the floodplain. Lake Pámpano, which was most strongly affected by local water, had the highest ratio of surface area to volume (ca. 1.5) and is positioned at the edge of the escarpment (flood boundary in Fig. 1), where runoff and groundwater inflows may be higher because of the greater slope and soil permeability. Lake Piña, which responded to a lesser degree, is also along the scarp, but its ratio of surface to volume is similar to that of Lake

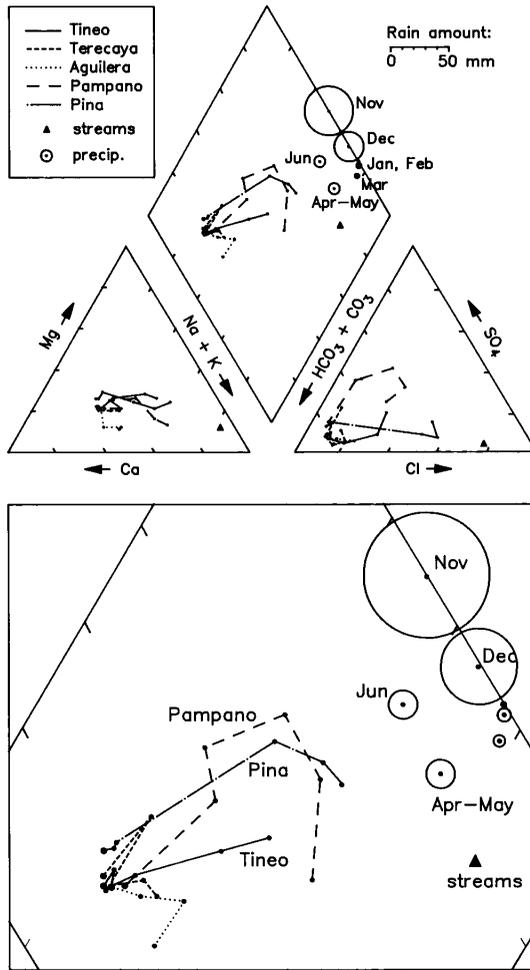


Fig. 9. Trilinear diagram showing changes in ionic proportions in five adjacent lakes over the course of isolation (1984—85). The upper field of the diagram is enlarged in the lower panel. The six lake sampling dates that are plotted here are 4 Nov (larger dot), 11 Nov, 18 Nov, 6 Jan, 25 Mar and 17 Jun. Volume-weighted means of precipitation chemistry were calculated at approximately monthly intervals, and the diameters of the circles are proportional to the amount of rain. The stream data are means for the samples collected near these lakes during 1988 (Table 9).

Tineo (ca. 0.9). Lake Piña also received water from adjacent lakes to the east, where several perennial streams enter the floodplain, and hence it is subject to the effects of storm runoff in an indirect and delayed manner. Lake Tineo may have been least affected because it is not adjacent to the escarpment during isolation and received no stream inflows. The relative importance of inputs of

local water to the lakes is thus difficult to assess without detailed knowledge of their basins and watersheds.

For the other Orinoco lakes, the direction of change in ionic proportions from inundation to isolation is generally toward the ionic proportions of local water, but substantial deviation is evident (Fig. 10). All of the lakes plot close together during inundation, then show considerable spread by late isolation. In particular, some lakes appear to gain sulfate (and lose bicarbonate) to a greater degree than can be explained by mixing with local waters. Lake Curita (site 12) and Lake Merecure (22) changed the most in ionic proportions; these two lakes had the lowest pH (5.4 and 4.1) at the end of isolation. The source of sulfate to the lakes may thus be sulfuric acid derived from mineral weathering. The three Caura lakes for which data are available change in a different direction than do the Orinoco lakes, and this change does not appear to be directed toward the ionic proportions of atmospheric deposition collected at the mouth of the Caura River (Fig. 11). We have no information on the chemistry of streams in this area.

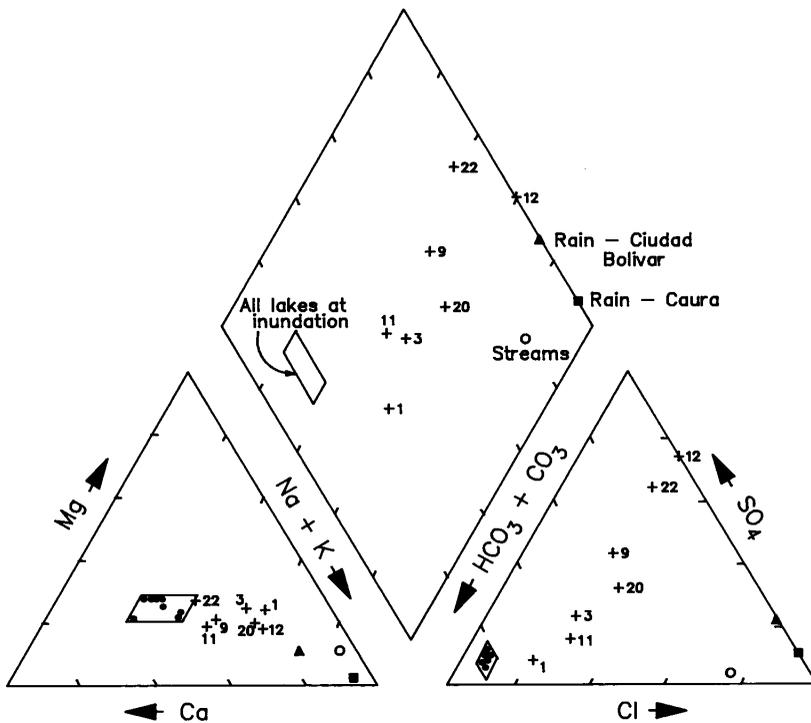


Fig. 10. Trilinear diagram comparing ionic proportions in a variety of Orinoco lakes at inundation (dots; Jul–Nov 1986) and at late isolation (pluses; Apr–May 1988). Lakes are identified by number in Table 1.

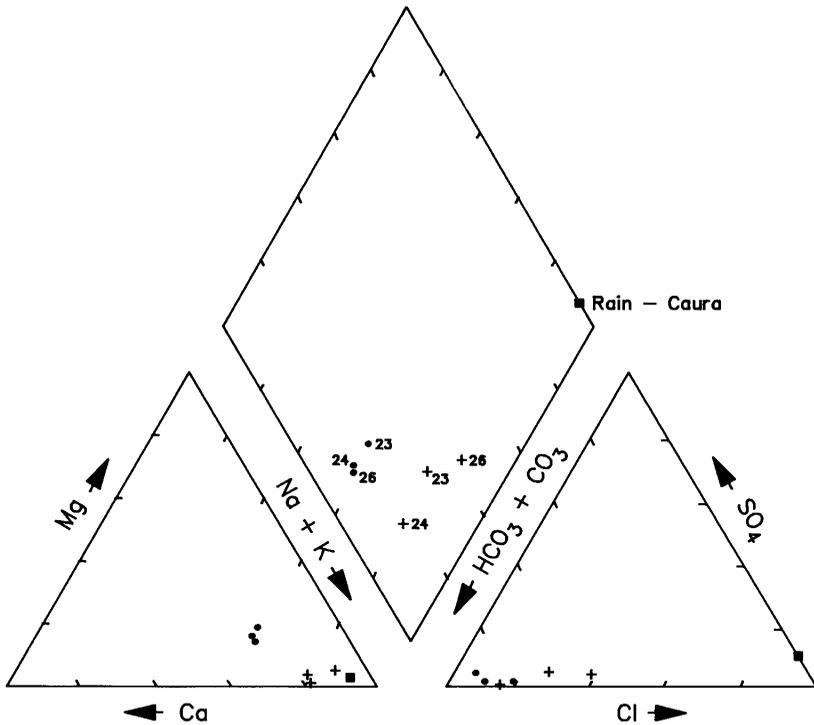


Fig. 11. Trilinear diagram comparing ionic proportions in several Caura lakes at inundation (dots; Jul–Nov 1986) and at late isolation (pluses; Apr–May 1988). Lake 23 = Paso Acosta; 24 = Paramuto; 26 = Madera.

Our observation that Orinoco floodplain lakes contain primarily river water at inundation, then become influenced to a variable degree by inputs of local water (rain and runoff) over the course of isolation is similar to the conclusions of FORSBERG *et al.* (1988) regarding floodplain lakes of the Amazon River. There are, however, notable hydrological contrasts between these two floodplain lake systems. The Amazon lakes sampled by FORSBERG *et al.* are generally larger and are often fed by perennial streams draining large upland basins. These lakes remain connected to the river throughout the year, and tend to drain into the river during low water in response to local water inputs, resulting in a flushing effect. Rainfall on the Amazon floodplain (ca. 2000 mm y^{-1} at Manaus) is about twice that of Ciudad Bolívar on an annual basis, and the dry season is much less pronounced (SCHMIDT 1972). For these reasons, the Amazon floodplain lakes sampled by FORSBERG *et al.* are more strongly influenced by inputs of local water, and many become filled entirely with local water by the end of the low-water phase, as these authors demonstrated using alkalinity as a tracer of water sources. FORSBERG *et al.* showed

that the ratio of drainage basin area to lake area was proportional to the importance of local inputs; we did not use this approach because for most Orinoco lakes it is difficult to define upland drainage basins in the flat mesas flanking the floodplain, and because there is so little runoff during isolation.

Relation between sediment resuspension and lake morphometry

Sediment resuspension is significant because it affects light, temperature and nutrient regimes (GABRIELSON & LUKATELICH 1985, DEMERS et al. 1987, HAMILTON & LEWIS 1987). The high turbidity that results can have both negative and positive consequences for the aquatic biota (MELACK 1985, GEDDES 1988, ENGLE & MELACK 1990). The intensity of resuspension is a function of several variables, including the wind velocity, effective fetch, depth of the water column, and physical properties of the sediments in areas of potential resuspension (HAKANSON & JANSSON 1983). Despite the complexity of the phenomenon, CARPER & BACHMANN (1984) demonstrated that sediment resuspension in a small lake was predictable from wind velocity.

We used the approach of CARPER & BACHMANN (1984) to relate wind velocity to sediment resuspension in Lake Tineo, for which we have extensive data. For floodplain lakes, wind velocity must be considered together with the continually decreasing water depth during isolation. Sediment resuspension increased in intensity over the course of the isolation phase in Lake Tineo (Fig. 5). Wind velocity was not measured at Lake Tineo, but data are available for the Venezuelan Air Force site in Ciudad Bolívar, located 9 km from the lake. These data should reveal general patterns in the area. The mean wind velocity (measured at Ciudad Bolívar) increased gradually until April and decreased thereafter (Fig. 12); maximum wind velocity (range, 7–17 m s⁻¹) shows a similar pattern. The wind during these months was consistently from the ENE (Venezuelan Air Force, unpublished data).

The theoretical depth of the base of deepwater waves is defined as the critical depth (Z_c) because, as deepwater waves enter water below this depth, the orbital paths of water motion contact the sediment surface and can cause sediments to be resuspended. The energy available for resuspension increases as the depth of the water column decreases further below the Z_c . To estimate the critical depth, we first calculated wave period (T , in s) from wind velocity by the empirical equation given by the U.S. Army Coastal Engineering Research Center (1977):

$$\frac{gT}{2\pi U} = 1.20 \tanh \left[0.077 \left(\frac{gF}{U^2} \right)^{0.25} \right]$$

where g is the gravitational constant (9.8 m s⁻¹ s⁻¹), U is the wind velocity (m s⁻¹; we used the mean from the 2 weeks prior to sampling) and F is the

effective fetch (m). The wavelength (L , in m) was determined from wave period:

$$L = \frac{gT^2}{2\pi}$$

The critical depth was assumed to be one-half of the wavelength.

The critical depth exceeded the mean depth of Lake Tineo throughout the isolation phase (Fig. 12), indicating that sediments could have been resus-

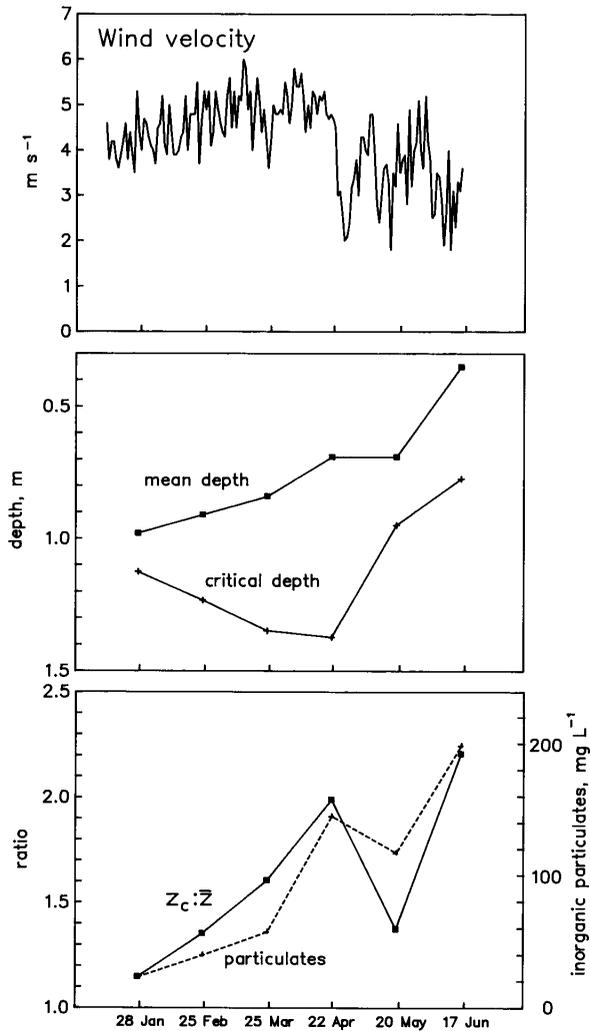


Fig. 12. Wind velocity, critical depth (Z_c), and sediment resuspension in Lake Tineo during the 1985 isolation phase. Wind velocity data are daily means calculated from measurements made at Ciudad Bolívar by the Venezuelan Air Force. Critical depth is explained in the text.

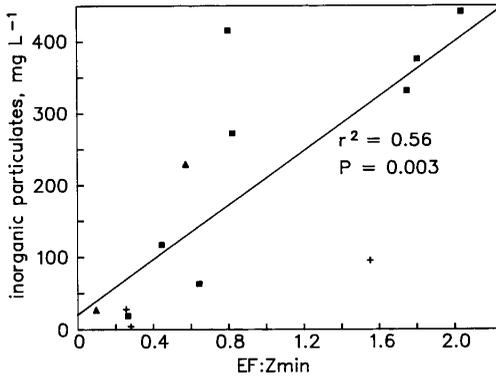


Fig. 13. Relationship between lake morphometry and the concentration of inorganic particulate material at late isolation (squares = Orinoco dish lakes, triangles = Orinoco channel lakes, pluses = Caura lakes). Resuspension of sediments elevates the concentration of inorganic particulates in many lakes at this time. $EF:Z_{min}$ = ratio of effective fetch (km) to minimum depth (m; depth at the center of a lake during its lowest water level). The regression equation is $Y = 182X + 27.64$.

pended from much of the lake bottom. The lower panel shows the ratio of critical depth to mean depth, superimposed on a plot of the concentration of inorganic particulates during this period. As expected, the ratio of critical depth to mean depth is directly related to the intensity of sediment resuspension because it reflects the increasing proportion of lake bottom from which sediments could be resuspended. This relationship suggests that sediment resuspension is predictable from wind velocity, effective fetch, and mean depth of Orinoco floodplain lakes.

The intensity of sediment resuspension in the other Orinoco floodplain lakes may be predictable if the effective fetch and depth of lakes are considered simultaneously, and if local variability in wind velocity is not great. For the lakes surveyed during isolation in 1988, little relation is apparent between sediment resuspension and effective fetch ($r^2 = 0.23$) or depth ($r^2 = 0.24$), but the relationship is improved using the ratio of effective fetch to depth ($r^2 = 0.56$; Fig. 13). Fetch determines the degree of wind-driven turbulence at the lake surface, while depth determines the degree to which this turbulent energy contacts the sediment surface. Consequently, some of the largest lakes may be too deep for sediment resuspension, and the fetch of the shallowest lakes may be too small for waves to develop.

Conclusions

Several important chemical and ecological characteristics of Orinoco floodplain lakes are predictable from lake basin morphology. However, at the present time, information contained in maps or aerial photographs yields only

very general predictions of lake characteristics, and prediction is better during inundation than during isolation of the lakes. Knowledge of lake depths significantly enhances predictive capabilities, as does information on the flow paths and chemistry of source waters for the lakes.

The distinction between dish lakes and channel lakes is useful in predicting the characteristics of Orinoco floodplain lakes during inundation. Channel lakes (length:width > 5) have detectable currents and short water residence times; their chemistry resembles that of the source water. When river water flows directly into channel lakes, there is little change in suspended particulates or in concentrations of labile nutrients, and phytoplankton growth is negligible. The chemistry of serial channel lakes reflects that of lakes upstream in the floodplain flow path. Dish lakes (length:width < 5) have relatively low rates of water movement and longer water residence times. They deviate in chemistry from the source water because of sedimentation of inorganic particulates, depletion of nitrate, and growth of phytoplankton. Also, dissolved oxygen can become depleted in dish lakes.

Caura floodplain lakes that we sampled are dish lakes, but because of the different chemistry of the source water, the extent of deviation from source water during inundation is less marked than for Orinoco lakes. Phosphorus limitation is probably significant in these lakes because of the extremely low concentrations of phosphorus in the Caura River.

During isolation, local waters (rain and runoff) contribute significantly to the water budget of many of the lakes. Lake morphology (particularly the ratio of surface area to volume) is one of several determinants of the importance of local waters to a given lake; other factors include position on the floodplain relative to the escarpment and the presence of perennial streams. Sediment resuspension occurs with increasing intensity over the course of the isolation phase because of the continual decrease in lake depths. The intensity of sediment resuspension in a lake is predictable from wind velocity, effective fetch, and the mean depth of the lake. Variation among lakes in the intensity of sediment resuspension during late isolation can be explained by variation in the ratio of effective fetch to depth, which provides a convenient index for prediction of sediment resuspension in Orinoco lakes.

Acknowledgements

This work results from a collaborative Venezuelan-U.S. study of the Orinoco River and its floodplain (Project PECOR, Proyecto Ecosistema Orinoco). Financial support was provided by the U.S. National Science Foundation (grants DEB8116725, BSR8315410, and BSR8604655). The Ministerio del Ambiente y de los Recursos Naturales Renovables and the Universidad Simón Bolívar provided important logistical support for our work in Venezuela.

We are grateful to M. RODRIGUEZ, S. RICHARDSON, S. TWOMBLY, A. HEYVAERT, C. WEBER, and M. GUZMAN for assistance in the field, to S. SIPPEL for field and analytical

work, to M. RODRIGUEZ and M. LASI for contributions of unpublished data, and to J. SAUNDERS for advice on data interpretation and for editorial comments. The final manuscript was improved by suggestions from two reviewers.

References

- ARMSTRONG, F. A. J. & BUTLER, E. I. (1962): Chemical changes in seawater off Plymouth during 1960. — *J. Mar. Biol. Assoc. U.K.* **42**: 253–258.
- CAHILL, R. A., AUTREY, A. D., ANDERSON, R. V. & GRUBAUGH, J. W. (1987): Improved measurement of the organic carbon content of various river components. — *J. Freshw. Ecol.* **4**: 219–223.
- CARPER, G. L. & BACHMANN, R. W. (1984): Wind resuspension of sediments in a prairie lake. — *Can. J. Fish. Aquat. Sci.* **41**: 1763–1767.
- DEMERS, S., THERRIault, J.-C., BOURGET, E. & BAH, A. (1987): Resuspension in the shallow sublittoral zone of a macrotidal estuarine environment: Wind influence. — *Limnol. Oceanogr.* **32**: 327–339.
- DRAGO, E. C. (1976): Mapa geomorfológico de la llanura aluvial del río Paraguay inferior. — *Revista de la Asociación Geológica Argentina* **30**: 217–222.
- ENGLE, D. L. & MELACK, J. M. (1990): Floating meadow epiphyton: Biological and chemical features of epiphytic material in an Amazon floodplain lake. — *Freshw. Biol.* **23**: 479–494.
- FORSBERG, B. R., DEVOL, A. H., RICHEY, J. E., MARTINELLI, L. A. & DOS SANTOS, H. (1988): Factors controlling nutrient concentrations in Amazon floodplain lakes. — *Limnol. Oceanogr.* **33**: 41–56.
- GABRIELSON, J. O. & LUKATELICH, R. J. (1985): Wind-related resuspension of sediments in the Peel-Harvey estuarine system. — *Estuar. Coast. Shelf Sci.* **20**: 135–145.
- GEDDES, M. C. (1988): The role of turbidity in the limnology of Lake Alexandrina, River Murray, South Australia; Comparisons between clear and turbid phases. — *Aust. J. Mar. Freshwater Res.* **39**: 201–209.
- GOULDING, M., CARVALHO, M. L. & FERREIRA, E. G. (1988): Rio Negro, rich life in poor water. — SPB Academic Publ.
- HAKANSON, L. (1981): A manual of lake morphometry. — Springer-Verlag, Berlin.
- HAKANSON, L. & JANSSON, M. (1983): Principles of lake sedimentology. — Springer-Verlag, Berlin.
- HAMILTON, S. K. & LEWIS, W. M. Jr. (1987): Causes of seasonality in the chemistry of a lake on the Orinoco River floodplain, Venezuela. — *Limnol. Oceanogr.* **32**: 1277–1290.
- HAMILTON, S. K., SIPPEL, S. J., LEWIS, W. M. Jr. & SAUNDERS, J. F. III. (1990): Zooplankton abundance and evidence for its reduction by macrophyte mats in two Orinoco floodplain lakes. — *J. Plankton Res.* **12**: 345–363.
- HARWOOD, J. E. & KUHN, A. L. (1970): A colorimetric method for ammonia in natural waters. — *Water Res.* **4**: 805–811.
- HEM, J. D. (1985): Study and interpretation of the chemical characteristics of natural water, 3rd ed. — U.S. Geological Survey Water-Supply Paper **2254**. 264 pp.
- HUTCHINSON, G. E. (1957): A treatise on limnology, 1: 1–1015. Geography, physics and chemistry. — John Wiley and Sons, Inc., New York; Chapman and Hall, Ltd., London.
- LEWIS, W. M. Jr. (1986): Nitrogen and phosphorus runoff losses from a nutrient-poor tropical moist forest. — *Ecology* **67**: 1275–1282.

- LEWIS, W. M. Jr. & GRANT, M. C. (1978): Sampling and chemical interpretation of precipitation for mass balance studies. — *Water Resources Res.* **14**: 1098—1104.
- LEWIS, W. M. Jr. & SAUNDERS, J. F. III. (1984): Cross-sectional variation in the chemistry and suspended sediment load of the Orinoco River at Ciudad Bolívar. — *Acta Científica Venez.* **35**: 382—385.
- — (1989): Concentration and transport of dissolved and suspended substances in the Orinoco River. — *Biogeochemistry* **7**: 203—240.
- LEWIS, W. M. Jr., HAMILTON, S. K., JONES, S. & RUNNELLS, D. (1987): Major element chemistry, weathering and element yields for the Caura River drainage, Venezuela. — *Biogeochemistry* **4**: 159—181.
- MARKER, A. F. H., NUSCH, E. A., RAI, H. & RIEMANN, B. (1980): The measurement of photosynthetic pigments in freshwaters and standardization of methods: Conclusions and recommendations. — *Arch. Hydrobiol. Beih., Ergebn. Limnol.* **14**: 91—106.
- MARNR (1983): Venezuela en mapas, 1st ed. — MARNR Dirección de Cartografía Nacional. Caracas.
- MARSH, P. & HEY, M. (1989): The flooding hydrology of Mackenzie Delta lakes near Inuvik, N.W.T., Canada. — *Arctic* **42**: 41—49.
- MEADE, R. H., NORDIN, C. F. Jr., HERNANDEZ, D. P., MEJIA, A. & GODOY, J. M. P. (1983): Sediment and water discharge in río Orinoco, Venezuela and Colombia, pages 1134—1144. — In: *Proceedings of the Second International Symposium on River Sedimentation*. Water Resources and Electric Power Press, Beijing, China.
- MELACK, J. M. (1984): Amazon floodplain lakes: Shape, fetch, and stratification. — *Verh. Internat. Verein. Limnol.* **22**: 1278—1282.
- (1985): Interactions of detrital particulates and plankton. — *Hydrobiologia* **125**: 209—220.
- MELACK, J. M. & FISHER, T. R. (1983): Diel oxygen variations and their ecological implications in Amazon floodplain lakes. — *Arch. Hydrobiol.* **98**: 422—447.
- MORRIS, M. D., BERK, J. A., KRULIK, J. W. & ECKSTEIN, Y. (1983): A computer program for a trilinear diagram plot and analysis of water mixing systems. — *Ground Water* **21**: 67—78.
- MURPHY, J. & RILEY, J. P. (1962): A modified single solution method for the determination of phosphate in natural waters. — *Anal. Chim. Acta* **27**: 31—36.
- NUSCH, E. A. (1980): Comparison of different methods for chlorophyll and phaeopigment determination. — *Arch. Hydrobiol. Beih., Ergebn. Limnol.* **14**: 14—36.
- PIPER, A. M. (1953): A graphic procedure in the geochemical interpretation of water analyses. — U.S. Geological Survey, Water Res. Div. Ground Water Notes, Geochemistry, no. 12. 14 pp.
- SARMIENTO, G. (1983): The savannas of tropical America, chap. 10. — In: F. BOURLIERE (ed.), *Tropical savannas. Ecosystems of the world* **13**. Elsevier.
- SAUNDERS, J. F. III. & LEWIS, W. M. Jr. (1988): Transport of phosphorus, nitrogen and carbon by the Apure River, Venezuela. — *Biogeochemistry* **5**: 323—342.
- — (1989): Transport of major solutes and the relationship between solute concentrations and discharge in the Apure River, Venezuela. — *Biogeochemistry* **8**: 101—113.
- SCHMIDT, G. W. (1972): Seasonal changes in water chemistry of a tropical lake (Lago do Castanho, Amazonia, South America). — *Verh. Internat. Verein. Limnol.* **18**: 613—621.
- SHELDON, R. W. (1972): Size separation of marine seston by membrane and glass-fiber filters. — *Limnol. Oceanogr.* **17**: 972—984.

- SOLÓRZANO, L. & SHARP, J. H. (1980): Determination of total dissolved nitrogen in natural waters. — *Limnol. Oceanogr.* **25**: 751–754.
- U.S. Army Coastal Engineering Research Center (1977): Shore protection manual, vol. I. — Fort Belvoir, VA.
- VALDERRAMA, J. C. (1981): The simultaneous analysis of total nitrogen and total phosphorus in natural waters. — *Mar. Chem.* **10**: 109–122.
- VAN ANDEL, T.J. H. (1967): The Orinoco Delta. — *J. Sed. Petrol.* **37**: 297–310.
- WEIBEZAHN, F. (1985): Concentraciones de especies químicas disueltas y transporte de sólidos suspendidos en el alto y medio Orinoco y sus variaciones estacionales. — Universidad Simón Bolívar (Caracas, Venezuela), Informe. 223 p.
- WELCOMME, R. L. (1985): River fisheries. FAO Fisheries Technical Paper **262**, Rome.
- WETZEL, R. G. & LIKENS, G. E. (1979): *Limnological analyses*. — Saunders, Philadelphia.
- WOOD, E. D., ARMSTRONG, F. A. J. & RICHARDS, F. A. (1967): Determination of nitrate in seawater by cadmium-copper reduction to nitrite. — *J. Mar. Biol. Assoc. U.K.* **47**: 23–31.

Submitted: 5 March 1990; accepted: 8 June 1990.