

Causes of seasonality in the chemistry of a lake on the Orinoco River floodplain, Venezuela¹

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Abstract

Lake Tineo, which lies on the Orinoco floodplain, passes through four seasonal phases (filling, through-flow, drainage, and isolation), during which the lake volume changes 20-fold. During filling and through-flow, when the lake is inundated by river water, floating grasses (*Paspalum repens*) and phytoplankton grow rapidly, causing depletion of inorganic N and P between inflow and outflow, although phytoplankton biomass does not accumulate because of flushing. Inundation of the surrounding forest has no quantifiable effects on concentrations of major ions or macronutrients. Following through-flow, phytoplankton biomass accumulates, and high abundances of blue-green algae increase N in the lake by fixation (15 kg ha⁻¹). Quantities of some elements released by decomposition of floating grasses over a 4-week period are very high in relation to lake-water inventories (K, 126%; Cl, 66%; organic C, 170%; N, 74%; and P, 89%). Mass balance for Lake Tineo shows, on an annual basis, net retention of N (27%)—partly because most nitrogen fixation is limited to the isolation phase—and P (39%), and net yield of inorganic C (24%). There is neither detectable net retention nor yield of organic C, major cations, sulfate, or chloride. The major chemical transformation of river water during passage through the lake is conversion of inorganic N and P to organic forms.

In the tropics, strong seasonal fluctuations in the physical and chemical characteristics of aquatic floodplain habitats contrast markedly with the relative environmental constancy of many other types of tropical waterbodies. Floodplain waterbodies, which are among the most important aquatic habitats in the tropics, appear to be fundamentally different from other kinds of aquatic habitats (Welcomme 1979). Pronounced seasonal cycles in water chemistry and biotic communities have been documented in studies of tropical floodplains such as those of the Amazon river system (reviewed in Sioli 1984), but the underlying abiotic and biotic causes of seasonality in such systems are frequently left to speculation because quantification of hydrology and mass transport is difficult.

The Orinoco River is one of a diminishing number of large rivers in the tropics that are as yet unregulated by impoundment and that retain a natural floodplain. Our purpose

here is to analyze seasonal cycles in the chemistry of a typical lake on the fringing floodplain of the lower Orinoco. We use a mass-balance model to relate changes in concentrations of major ions and nutrients to mass transport, water balance, and abiotic or biotic processes within the lake, with the purpose of identifying the primary causes of seasonality in the lake.

Lake Tineo (8°12'N, 63°28'W) is a lateral levee lake (Hutchinson 1957) located along the Orinoco River, 8 km from Ciudad Bolívar, Venezuela (Fig. 1). Seasonal extremes of surface area are shown in Fig. 1. The low-water boundary in the figure also corresponds roughly to the open-water area at high water. No streams drain into the lake from its watershed of 22 km². During inundation, Lake Tineo remains spatially discrete from the river and from adjacent lakes. Two channels carry water across a levee between the river and the lake, and another channel connects Lake Tineo to Lake Piña (Fig. 1). All of these connections are dry at low water. In relation to the river, Lake Tineo has four hydrological phases: filling, through-flow, drainage, and isolation.

Average annual precipitation measured by the Venezuelan Air Force at Ciudad Bolívar (9 km southwest of the lake) is 983

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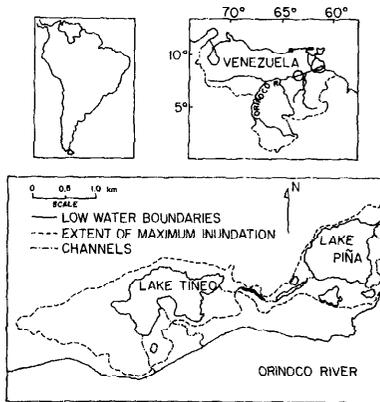


Fig. 1. Location of the study site.

mm. In most years, including the study period, 85–90% of the precipitation occurs from May to November, when most floodplain lakes are connected with the river. The floodplain forest that grows on seasonally inundated land around Lake Tineo can be classified as seasonal *várzea* forest according to Prance's (1979) system for the Amazon. *Trachypogon* savanna with patches of deciduous forest covers higher ground that is not seasonally inundated.

The only abundant macrophyte in Lake Tineo is *Paspalum repens* Berg (Gramineae), a semiaquatic grass. In Lake Tineo, this grass grows along the edge and in clearings of the floodplain forest but not in open water. At low water, remnant populations of *P. repens* persist on shore, rooted in the mud. Upon inundation, these plants grow up from the substrate and float at the water surface. Rapid growth continues until seeds are produced at high water (September–October). Although most of the plants die at falling water (October–December), a reduced population survives on the banks of the lake throughout the dry season. This seasonal pattern is similar to that described by Junk (1970) for *P. repens* on the Amazon floodplain.

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Methods

Sample collection—Water samples and field measurements at the lake were taken between 17 June 1984 and 17 June 1985. On each sampling date, dissolved oxygen (meter: ± 0.1 mg liter⁻¹), temperature (meter: $\pm 0.6^\circ\text{C}$), and light transmission (spherical quantum sensor: PAR) were measured in the afternoon at the center of the lake. A flexible plastic tube of 7.5-cm diameter was used to collect an integrated sample from the surface to the bottom of the mixed layer, which corresponded to most or all of the water column. One subsample for chemical analysis was stored on ice and filtered within 2 h; a second subsample for phytoplankton cell counts was preserved in the field with Lugol's solution.

The chemistry of integrated river samples collected monthly at Ciudad Bolívar, just above the lake, was used in mass transport calculations to represent river water that entered the lake. The river samples provide good estimates of inflow of dissolved substances, but probably result in overestimation of the inflow of particulate materials, which are more concentrated in the core area of the river channel (Lewis et al. 1984). Water that entered Lake Tineo from adjoining Lake Piña during the filling phase was sampled along the channel between the two lakes. Transport of substances in the outflow from Lake Tineo was estimated from the chemistry of water at the lake sampling site.

Samples of bulk atmospheric deposition were collected at biweekly intervals from a collector of the type described by Lewis and Grant (1978), slightly modified to prevent birds from perching on the collector. The collector was situated on a barge near the north bank of the river, 14 km west of the lake. Floating grasses were sampled in October 1985 at three sites around the shoreline of the lake for identification and analysis of elemental composition.

Variation in physical and chemical variables across the lake was investigated at high water (16 September) and at low water (30 December). At seven sites located throughout the lake, samples were collected in duplicate by the same methods used in routine

sampling. Vertical spatial variation was surveyed twice during periods of weak thermal stratification (14 October and 11 November). Samples were collected at 0.5-m intervals with a Van Dorn sampler for comparison with the integrated samples. At other times, profiles of temperature and dissolved oxygen indicated that the water column was well mixed.

Laboratory analyses—Alkalinity was estimated on unfiltered water by incremental titration (Wetzel and Likens 1979). Samples were filtered 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 particulate material. Carbon and nitrogen on the filter were measured with an elemental analyzer; another GF/C filter containing particulate material was analyzed for particulate phosphorus (Solórzano and Sharp 1980). Filtered samples were analyzed for calcium, magnesium, sodium, and potassium by flame atomic absorption and for chloride and sulfate by ion chromatography.

Analyses for labile soluble components were completed the day after collection, and digestions for the analyses of soluble organic carbon, nitrogen, and phosphorus were completed within 2 d. The sum of nitrate and nitrite was determined by cadmium-copper reduction of nitrate followed by colorimetric analysis of nitrite (Wood et al. 1967). Occasional analyses showed that nitrite concentrations remained below detection limits ($< 1 \mu\text{g liter}^{-1}$). Ammonium was analyzed by the phenolhypochlorite technique (Harwood and Kuhn 1970). Total soluble nitrogen was determined by persulfate digestion followed by analysis for nitrate (Valderrama 1981). Soluble organic nitrogen was calculated by subtraction of nitrate and ammonium from total soluble nitrogen, and total nitrogen was calculated as the sum of the total soluble and particulate fractions.

Soluble reactive phosphorus was analyzed by the ascorbic acid-molybdate method (Murphy and Riley 1962). Total soluble phosphorus was determined by persulfate digestion, in combination with the total soluble nitrogen analysis, followed by analysis for soluble reactive phosphorus. Soluble un-

reactive phosphorus was calculated by subtraction of soluble reactive phosphorus from total soluble phosphorus, and total phosphorus was calculated as the sum of the total soluble and particulate fractions.

Samples of floating grasses were dried at 95°C, milled to pass through a 0.5-mm mesh, dry-ashed (Allen et al. 1974), and analyzed for calcium, magnesium, sodium, and potassium by flame atomic absorption. Nitrogen and phosphorus in the grass samples were analyzed by the same methods used to analyze particulate material on filters. Carbon was estimated from loss on ignition (Allen et al. 1974). Phytoplankton were identified and counted with an inverted microscope. Heterocysts were counted in subsamples of the phytoplankton samples taken during the drainage and isolation phases when heterocystous algae were abundant.

Water budget and mass-balance model—The volume of the lake on each sampling date was calculated by the method of Hakanson (1981) from data on area (by vertical aerial photography), bathymetry (by echo sounding), and water level (by staff gauge). During inundation of the lake, either inflow (filling phase) or outflow (through-flow and drainage phases) was calculated as the residual term of the water budget. During the through-flow phase, discharges in the channels that carried water from the river into the lake were calculated from cross-sectional areas and current velocities (Price-type meter) measured weekly. Rainfall on the surface of the lake was calculated from daily rainfall at Ciudad Bolívar. Overland runoff was considered to be unimportant because rainfall on the lake surface agreed well with observed increases in lake level when the lake was isolated. Groundwater flow was assumed to be zero; this assumption is supported by a chemical comparison of local groundwaters with lake water, as explained below.

Several sources of data on evaporation were considered for the water budget. Daily measurements of evaporation from a Wild evaporimeter (Nemec 1964) were available for Ciudad Bolívar. Independent estimates were also obtained with the U.S. Weather Bureau nomograph for estimating evapo-

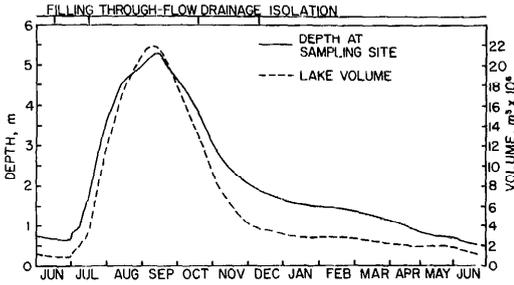


Fig. 2. Depth and volume of Lake Tineo during the study.

ration from shallow lakes (Kohler et al. 1955), which yielded values within 10% of the evaporimeter data. For the isolation phase, we also estimated evaporation from the observed changes in lake level, corrected for small amounts of precipitation. In the absence of significant groundwater flow, this method is more accurate. The evaporation estimates based on lake level were within 10% of the other two estimates. We used the evaporimeter data for the water budget except during the isolation phase, for which we used the evaporation estimates based on lake level.

Seasonal patterns in concentrations of major ions and nutrients in the lake were interpreted with a mass-balance model based on the water budget. The mass of each substance in the lake was calculated for 24 June, just prior to inundation. For ensuing dates, mass in the lake was modeled as

$$M_e = M_b + M_i + M_d - M_o$$

where M_e is the predicted mass in the lake, M_b the initial mass in the lake, M_i the ad-

vective mass transport into the lake, M_d the bulk atmospheric deposition, and M_o the advective mass transport out of the lake. We compared observed and predicted concentrations for a conservative substance (sodium) as a means of quantifying error that is inherent in the model and therefore common to all of the substances that are modeled. Symmetrical 95% confidence bands around the model concentrations were derived from the relative errors (ratio of mean absolute deviation to predicted concentration) normalized by log transformation. For a given substance, deviations of observed concentrations from model concentrations are considered significant (interpretable) only if observed concentrations are outside the 95% confidence bands and if the pattern of deviation is systematic. Such deviations are assumed to be caused by factors other than mass transport and water balance.

Results

Morphometry, hydrology, and spatial variation—Changes in lake depth and volume are depicted in Fig. 2, and the water budget is summarized in Table 1. During the filling phase (17 June–30 July), water entered the lake directly from the river through two channels and to a small extent also through a third channel from Lake Piña, which had filled with river water several weeks earlier. The lake boundary began to enter the surrounding forest during filling. On 30 July, flow in the channel from Lake Piña reversed, establishing an outflow and beginning the through-flow phase. The re-

Table 1. Water budget (10^6 m^3) for Lake Tineo during the study.

	Filling (17 Jun–30 Jul)	Through-flow (30 Jul–4 Nov)	Drainage (4 Nov–30 Dec)	Isolation (30 Dec–17 Jun)
Inflow, river	8.8*	155.8	0	0
Inflow, Piña	1.5	0	0	0
Rainfall	0.5	2.4	0.8	0.5
Total gain	10.8	158.2	0.8	0.5
Outflow, river	0	0	5.3*†	0
Outflow, Piña	0	158.9*	—	0
Evaporation	0.3	2.4	0.7	2.1*
Total loss	0.3	161.3	6.0	2.1
Net storage	+10.5	−3.1	−5.2	−1.6

* Calculated from the water balance.

† Includes both the river and Lake Piña.

tention time of water in the lake during through-flow reached a minimum of 7 d during September. Rainfall was unimportant to the water budget or chemistry of the lake during inundation because of the high inflow of river water.

The falling river level caused flow in the channels between the lake and the river to reverse, initiating the drainage phase, around 4 November. During drainage the lake boundaries retracted from the forested area. Outflow decreased gradually throughout the drainage phase until it ceased on 30 December. The ensuing isolation phase lasted through June 1985. The lake volume decreased by about 50% during the isolation phase because evaporative water loss exceeded rainfall on the lake (Fig. 2, Table 1). Rainfall significantly affected the water budget and chemistry of the lake during the isolation phase.

The surveys for variation in physical and chemical variables across the lake support the assumption of the mass-balance model that the central sampling site adequately represents the lake. In the high-water survey, the coefficients of variation (CV: $100 \times s/\bar{X}$) among the seven sites were <6% for all of the major ions except chloride (16%). The CVs were higher for nitrate (27%), soluble reactive phosphorus (31%), particulate nitrogen (34%), and particulate carbon (22%), but no common spatial pattern was evident in this variation among sites. In the low-water survey, the CVs among the seven sites were <2% for all of the major ions except sulfate (12%). The only variable with a CV >12% was ammonium (28%). The CVs for nitrate and soluble reactive phosphorus could not be determined because concentrations were below our analytical detection limit ($<1 \mu\text{g liter}^{-1}$). The random nature of the spatial variation indicates that it may cause minor irregularities in the temporal patterns of some variables, but that it is unlikely to cause systematic error in the mass-balance model.

Surveys of vertical variation on two dates when there was thermal stratification support our assumption that the integrated samples represent the entire water column. Comparison of the integrated sample with discrete samples taken near the bottom on

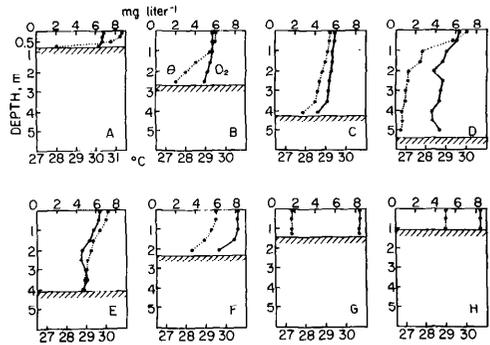
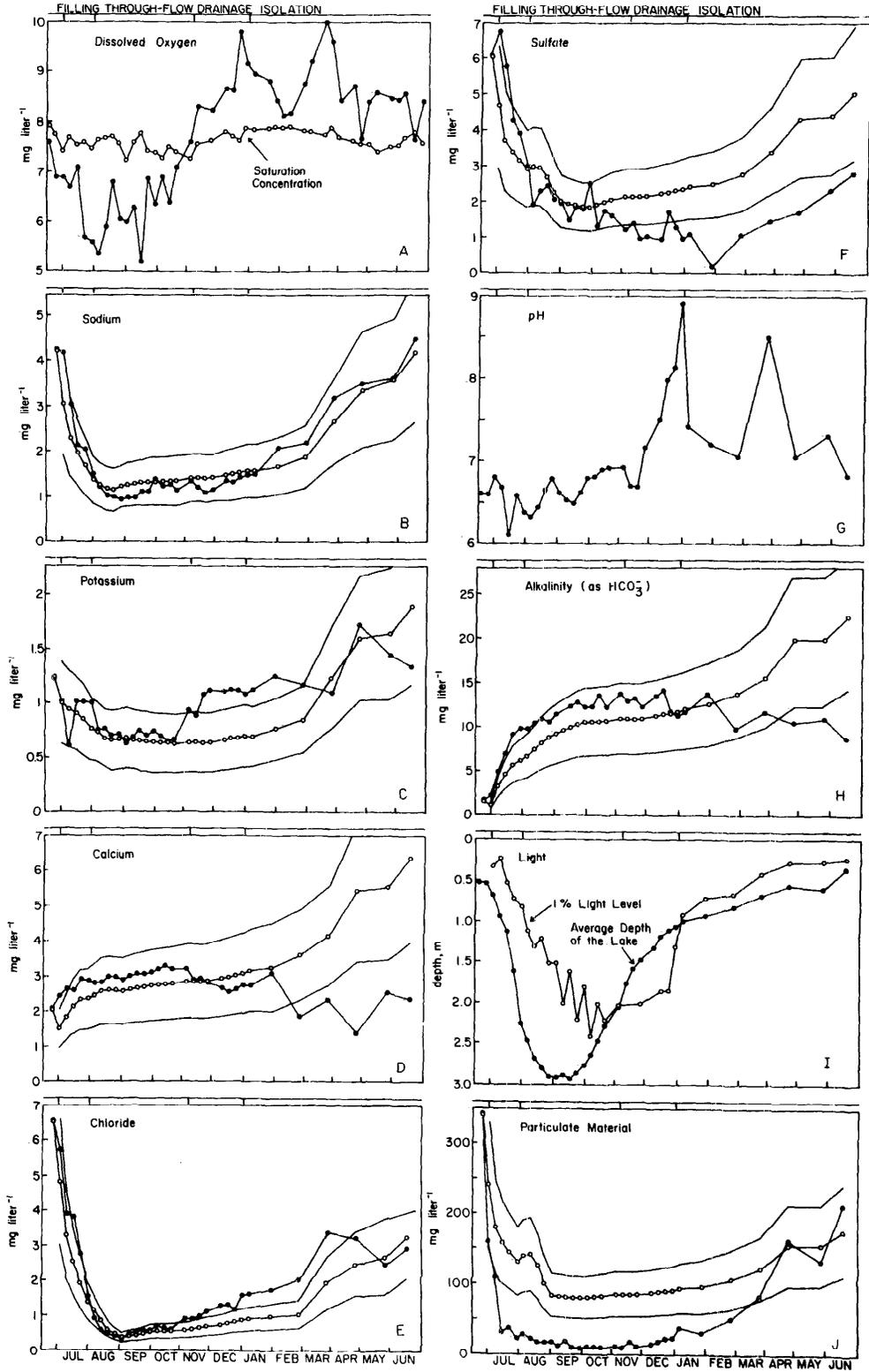


Fig. 3. Representative vertical profiles of temperature (dotted line) and dissolved oxygen (solid line). A. Isolation phase (1 July). B. Filling (22 July). C. Early through-flow (12 August). D. Mid-through-flow (9 September). E. Late through-flow (14 October). F. Drainage (25 November). G. Isolation (28 January). H. Isolation (1 April).

14 October showed no significant differences for soluble components. Concentrations of particulate nitrogen and carbon in the integrated sample were twice those near the bottom on 14 October, probably as a result of higher phytoplankton densities near the surface. On 11 November, both particulate and soluble materials were well mixed vertically.

Temperature, oxygen, and major ions—During the filling and through-flow phases, surface waters were consistently below saturation for dissolved oxygen (Figs. 3, 4A). There were often weak vertical gradients of temperature and dissolved oxygen between 15 July and 25 November, when depth at the sampling site was >2 m (Fig. 3). These gradients apparently persisted for short but variable periods, depending on the weather. Persistent, severe deoxygenation of water near the bottom was not observed in the open-water area of the lake. Continual inflow of river water probably reduced the likelihood of stratification and was a source of oxygen to the bottom waters. Occasional measurements in the flooded forest also showed no evidence of anoxic waters, but because much of the forest was impenetrable, we do not know if anoxia occurred in the densely vegetated areas. During the drainage and isolation phases, surface waters were almost always above saturation for dissolved oxygen in the afternoon (Fig. 4A),



and uniform profiles of temperature and dissolved oxygen indicated that the water column usually mixed daily (Fig. 3).

The concentration of sodium in the lake followed the model concentration throughout the year (Fig. 4B), demonstrating that the model accurately predicts patterns for a conservative substance. The good agreement for sodium confirms our assumption that groundwater flow is unimportant to the water budget of the lake. Groundwaters throughout the area are of the sodium-bicarbonate type or, less often, of the sodium-chloride type (Acosta et al. 1978). Even a small groundwater inflow would cause the observed sodium concentration to deviate from the model concentration during isolation because sodium concentrations in local groundwaters are considerably higher ($21\text{--}36\text{ mg liter}^{-1}$) than the sodium concentration in the lake (Fig. 4B). Also, if groundwater outflow (seepage) were important, then the observed concentration of sodium during the isolation phase, when decreases in lake volume are assumed to be caused solely by evaporation, would be below the model concentration.

Of the other major ions, only magnesium ($0.6\text{--}1.0\text{ mg liter}^{-1}$) was conservative throughout the year. Potassium was conservative during through-flow, but the concentration nearly doubled between 21 October and 25 November (drainage phase, Fig. 4C) by means other than transport. The concentration of calcium in the lake decreased relative to the model concentration during the drainage and isolation phases (Fig. 4D). Chloride was conservative until the drainage phase (Fig. 4E), when the concentration in the lake increased in a pattern similar to that of potassium. The concentration of sulfate in the lake decreased relative to the model concentration during the drainage and early isolation phases (Fig. 4F), then rose steadily throughout the remainder of the isolation phase at a rate greater than that predicted on the basis of evaporative concentration of the lake water.

Other variables—Until the late drainage phase, the pH of the lake water (6.65–7.10) resembled that of river water. The pH then increased rapidly (Fig. 4G). Alkalinity decreased relative to model concentrations throughout the late drainage and isolation phases (Fig. 4H). The extremely low alkalinity of the water before inundation of the lake in June 1984 indicates a similar steady loss of bicarbonate during the preceding isolation phase.

The lake was very turbid before inundation (Fig. 4I, J), when the suspended particulate material was only 2–3% carbon (Fig. 5A). During the filling and through-flow phases, particulate material sedimented. Light transmission reached a maximum during the late through-flow phase, when inflow of turbid river water was decreasing, and remained high throughout the drainage phase, when the entire water column was euphotic. The suspended particulate material contained a higher proportion of carbon (10–22%) during the late through-flow and drainage phases than at other times. Resuspension of sediments by wind-induced turbulence increased the concentration of inorganic particulate material in the water column as the lake became very shallow late in the isolation phase. Sediment resuspension intensified as the depth of the lake continued to decrease throughout the isolation phase, until by 17 June the euphotic zone was only 0.13 m thick, and the suspended particulate material was 3% carbon.

The concentration of nitrate was high before inundation, then rapidly dropped as the lake filled and remained low for most of the year (Fig. 5B). The concentration of ammonium in the lake was consistently higher than the model concentration during the filling, through-flow, and early drainage phases, and later decreased during the late drainage and isolation phases (Fig. 5C). Ammonium was usually present in excess of nitrate; the concentration of nitrate was higher only during the late isolation (June) and early filling phases. Compared with the

Fig. 4. A. Dissolved oxygen concentrations measured at 0.1 m, with the corresponding saturation concentrations at temperatures in situ. B. Sodium; observed concentrations (●) and model concentrations (○), with 95% C.L. C, D, E, F, H, J. Results for other modeled substances are depicted as for sodium. G. pH. I. Depth of the euphotic zone and average depth of the lake.

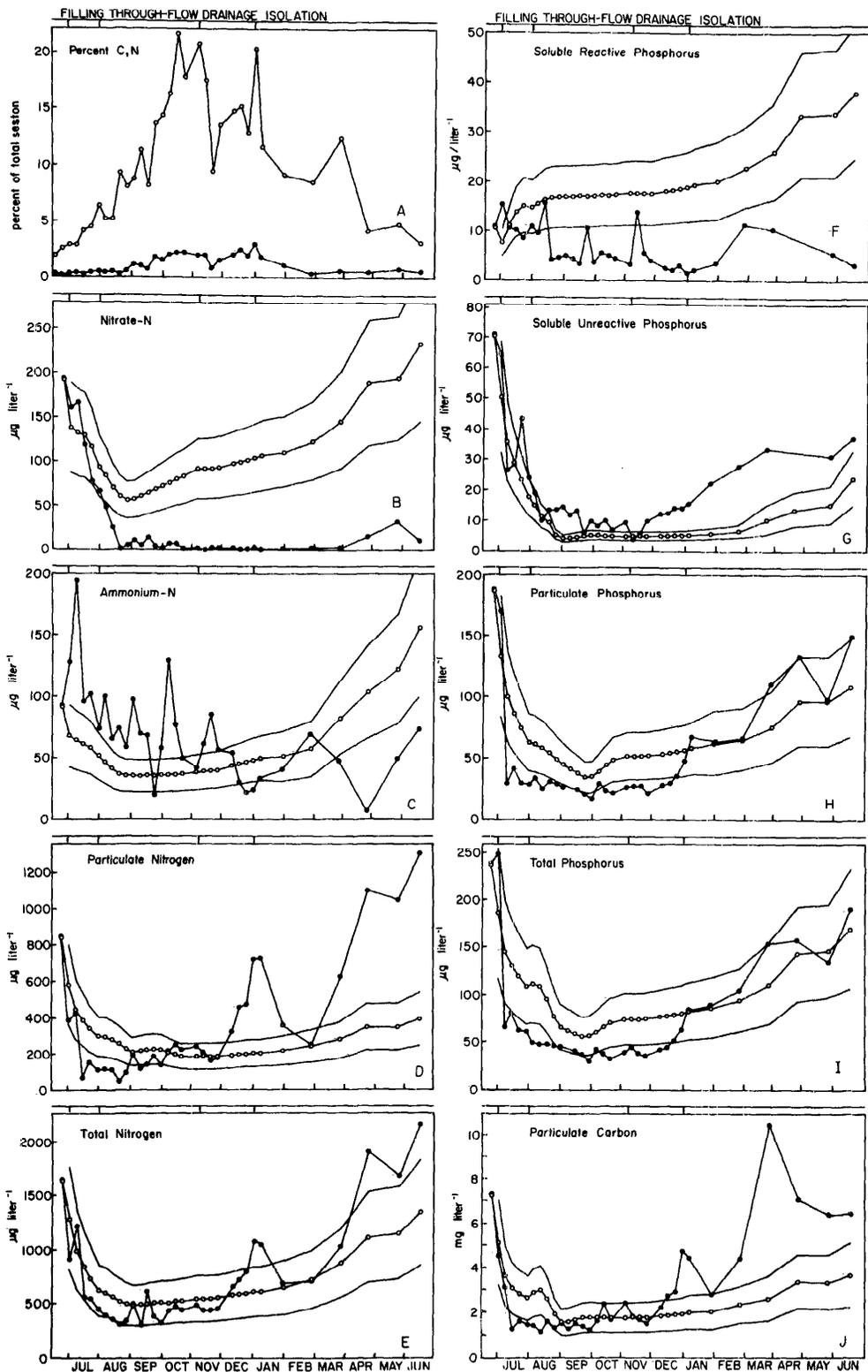


Fig. 5. A. Percent C and N in the seston. B-J. Other substances depicted as in Fig. 4B.

Table 2. Elemental budgets (in t) for Lake Tineo between 17 June 1984 and 17 June 1985.

	Transport in	Transport out
Calcium	436.3	489.5
Magnesium	95.7	115.5
Sodium	214.7	181.1
Potassium	114.3	119.4
Chloride	87.7	90.7
Sulfate	355.4	308.5
Inorganic C	1,539	1,911
Organic C	1,111	1,000
Nitrogen	85.3	62.5
Phosphorus	11.0	6.7

concentration in river water, the concentration of nitrate in the lake was much lower, and the concentration of ammonium in the lake was higher.

The concentration of soluble reactive phosphorus was consistently lower than the model concentration (Fig. 5F), and the concentration of soluble unreactive phosphorus was generally higher (Fig. 5G). Major increases in the amount of soluble unreactive phosphorus that were not accounted for by mass transport occurred before the late drainage phase; evaporative concentration of the lake water accounts for the later steady increase in concentration during the isolation phase.

Soluble organic nitrogen (100–600 $\mu\text{g liter}^{-1}$) and soluble organic carbon (4–11 mg liter^{-1}) were conservative, indicating the refractory nature of much of the soluble organic matter. The concentration of particulate nitrogen (Fig. 5D), phosphorus (Fig. 5H), and carbon (Fig. 5J) followed the pattern of total particulate material (Fig. 4J) during inundation. Peaks in these variables during the isolation phase were not related to the pattern of total particulate material, however. Patterns of total nitrogen (Fig. 5E) and total phosphorus (Fig. 5I) were similar to those of the particulate fractions of these elements.

Element budgets and nutrient processing—Over 95% of the annual transport of substances through the lake occurred during the 14-week through-flow phase. As a result, errors in the estimation of transport of elements through the lake during this period, which are too small to affect our interpretation of seasonal patterns, might affect the

annual budget calculations significantly (10–20%). Net gains and net losses as shown in Table 2 are indistinguishable from zero within our error limits for sodium, potassium, calcium, magnesium, chloride, sulfate, and total organic carbon. The annual budgets provide evidence for net retention of nitrogen and phosphorus and for net yield of inorganic carbon, but the variance attached to these net fluxes is high.

Transformations of carbon, nitrogen, and phosphorus during passage of river water through Lake Tineo indicate floodplain processes that are potentially important to river chemistry. For organic carbon, the ratios of soluble to particulate fractions in outflow and inflow were very similar. Nitrogen that entered the lake was 13% nitrate and 7% ammonium. Loss of nitrate and gain of ammonium in the lake changed outflowing nitrogen to 2% nitrate and 18% ammonium. However, proportions of soluble organic nitrogen and of particulate nitrogen were similar in inflow and outflow. Phosphorus entering the lake was 26% soluble reactive, 7% soluble unreactive, and 67% particulate. After passage of river water through the lake, the phosphorus in the outflow was 14% soluble reactive, 25% soluble unreactive, and 61% particulate.

Phytoplankton and floating grasses—Phytoplankton densities were low during the filling, through-flow, and early drainage phases (Fig. 6). During the drainage phase, cell densities increased greatly and remained high throughout the isolation phase. Blue-green algae dominated the phytoplankton during most of the year. Colonial forms were particularly abundant during the blooms of the late drainage and isolation phases. Nitrogen fixers such as *Anabaena catenula* and *Anabaenopsis circularis* were abundant during the drainage and isolation phases. During periods of high inorganic turbidity caused by resuspension of sediments (Fig. 4I), the proportion of blue-greens in the phytoplankton decreased, and diatoms became more abundant. High turbidity and continuous mixing of the water column probably limited light availability to phytoplankton and resulted in the low cell densities at the beginning of the study (June and July).

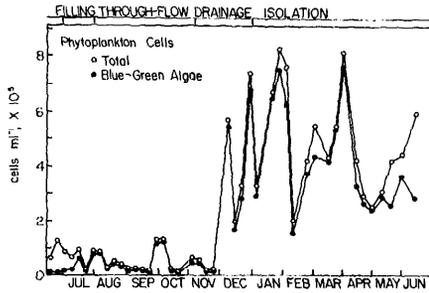


Fig. 6. Abundances of blue-green algae and of total phytoplankton.

The peaks in total (mainly particulate) nitrogen during the drainage and isolation phases (Fig. 5E) occurred when nitrogen-fixing blue-green algae were abundant in the lake. Mass-balance data indicate that 15 kg N ha^{-1} was added to the lake from sources other than transport between December and May. Heterocyst densities, which were converted to whole-lake abundances to facilitate comparison with the nitrogen data, correspond to increases in total nitrogen in the lake water that were not accounted for by mass transport (Fig. 7).

Analysis of the elemental content of the floating grass *P. repens* in Lake Tineo showed that it contained 0.02% sodium, 1.51% potassium, 0.34% calcium, 0.18% magnesium, 1.35% nitrogen, and 0.10% phosphorus on a dry-weight basis. Similar elemental ratios are reported by Howard-Williams and Junk (1976) for *P. repens* from an Amazon floodplain lake. The dry weight of the grass samples was 15.3% ash and therefore about 38% carbon (Allen et al. 1974).

Discussion

The correspondence between model and observed concentrations for many variables during much of the year in Lake Tineo reflects the strong influences of mass transport, dilution and flushing with river water, and evaporative concentration on the chemistry of the lake. In addition, however, some other important factors are identifiable after the effects of mass transport and water balance are made evident through use of the mass-balance model, including mixing, sediment-water interactions, and growth of floating grasses and phytoplankton.

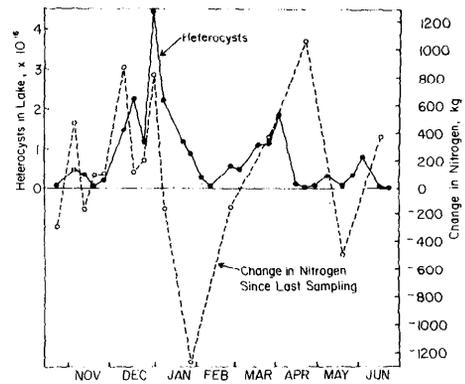


Fig. 7. Total heterocysts in the lake and the change in total nitrogen in the lake (after accounting for transport) during the preceding interval.

The open-water area of Lake Tineo mixed continuously throughout the year (Fig. 3), thus preventing the development of an anoxic hypolimnion. Oxygen at the sediment-water interface reduces the movement of solutes from the sediments (Mortimer 1971) and allows greater biological activity at the sediment surface. Persistent thermal stratification and development of an anoxic hypolimnion have been reported in floodplain lakes of the Amazon during high water (Schmidt 1972; Melack and Fisher 1983; Tundisi et al. 1984). The Amazon lakes that have been studied are deeper at high water (6–12-m max) than Lake Tineo and apparently have lower rates of through-flow. Stratification persists in the Amazon lakes when the depth exceeds 5–6 m; Lake Tineo has a maximum depth of 5.5 m. The short residence time of water in Lake Tineo during through-flow would also reduce the likelihood of stratification; we have observed anoxic water near the bottom in other Orinoco floodplain lakes similar to Lake Tineo but with less through-flow.

Interaction between the mixing regime and the seasonal fluctuation in depth of the lake results in sedimentation of particulate material at high water and resuspension of sediments at low water. These processes control the depth of the euphotic zone (Fig. 4I) and probably affect the availability of nutrients to phytoplankton, which can utilize nutrients adsorbed to particles (Grobelaar 1983; Setaro and Melack 1984). Seasonal alternation of sedimentation and

resuspension have been documented in other floodplain lakes (Schmidt 1973; Vásquez and Sánchez 1984). Maximum total resuspension in Lake Tineo was 210 g m^{-2} . Given a density equal to that of a clay sediment ($1.09 \text{ g dry wt cm}^{-3}$; Hakanson and Jansson 1984), resuspension of only 0.2 mm of sediment would have caused the observed increase in total particulate material in the water column.

The period of rapid growth of floating grasses (July–September) corresponds with the filling and most of the through-flow phases. During this period, nutrients assimilated from influent river water by the grasses are retained within the lake, in contrast to nutrients in phytoplankton biomass, which are continuously exported (albeit in a different fraction) back to the river through surface outflows. Most of the grasses die in late October and November, when through-flow is reduced or nonexistent. Nutrients released through decomposition of these grasses are therefore retained in the lake or in surrounding soils, except for losses through surface outflow during the drainage phase. Thus the grasses function as a nutrient trap in floodplain lakes (Furch 1984a), retaining nutrients from water passing through the floodplain and later adding them to the available nutrient inventory of the floodplain during the drainage and isolation phases.

Floating grasses covered about 5% (39 ha) of Lake Tineo at high water, as estimated from vertical aerial photographs. The average density of mats of *P. repens* in Lake Tineo is $7.6 \text{ t dry mass ha}^{-1}$, which falls within the range of $6\text{--}8 \text{ t ha}^{-1}$ reported by Junk (1970) for this species in the Amazon floodplain. Thus we estimate that about 296 t dry mass of *P. repens* developed during inundation in Lake Tineo. Assimilation by grasses did not affect the concentrations of major ions during the filling and through-flow phases (Fig. 4), but must have contributed to the observed decreases of nitrate and soluble reactive phosphorus (Fig. 5B, F). An estimated 10.0 t of nitrate-N and 1.9 t of soluble reactive phosphorus were lost or transformed in the lake during filling and through-flow; from our data on biomass and elemental content, we estimate that the

growth of *P. repens* would have required 4.0 t of nitrogen and 0.3 t of phosphorus.

The release of elements during the decomposition of floating grasses can also be estimated. The grasses would have released 4.3 t of potassium, assuming decomposition rates similar to those shown for *P. repens* in the Amazon (Howard-Williams and Junk 1976). Between 21 October and 25 November, 3.6 t of potassium was added to the lake. This gain in potassium, which was not accompanied by major gains in the other major cations, can thus be accounted for entirely by decomposition of grasses. Furch et al. (1983) also found that concentrations of potassium in particular increased during macrophyte decomposition in an Amazon floodplain lake.

The concentration of chloride, which is normally a conservative ion in lakes, increased over the model concentration (Fig. 4E) during the same period as the potassium increase (21 October–25 November); 2.3 t of chloride was added to the lake during this period. No data are available on the chlorine content of *P. repens*. Potassium and chlorine contents of a wide variety of North American aquatic macrophytes are correlated, however (Hutchinson 1975). The average mass ratio for potassium to chlorine in various floating-leaved plants is 1.31 (Riemer and Toth 1968; Cowgill 1974), which corresponds well to the mass ratio of potassium to chloride added to the lake waters between 21 October and 25 November (1.57). We therefore conclude that decomposition of the grasses was responsible for the addition of chloride to the lake.

Decomposition of the grasses during the drainage phase would also have released 1.67 t of nitrogen and 0.16 t of phosphorus. By comparison, on 25 November the lake water contained 2.33 t of nitrogen and 0.18 t of phosphorus. Given that the grass loses 57% of its original dry weight in the first 14 d of decomposition (Howard-Williams and Junk 1976), it is likely that roughly half (51 t) of the carbon content of the grass is released to the lake. This release is substantial in comparison to the 30 t of organic carbon in the lake water on 25 November.

During the filling and through-flow phases, phytoplankton did not significantly af-

fect dissolved oxygen, which remained below saturation, or pH, which differed little from that of river water. However, much of the reduction in concentrations of nitrate and soluble reactive phosphorus as river water flowed through the lake was evidently caused by phytoplankton, as shown by the calculation of nutrient storage in the grasses, which can account for only 40% of the nitrogen conversion and 16% of the phosphorus conversion. Periphyton is probably less important than phytoplankton during inundation in Lake Tineo because of the relatively small area of potential habitat; most of the inundated forest is heavily shaded, and sediments under open waters were usually below the euphotic zone (Fig. 4I). During the drainage and isolation phases, when phytoplankton densities were much higher (Fig. 6), phytoplankton photosynthesis resulted in continual supersaturation of the water with dissolved oxygen, depletion of inorganic carbon, and increase of pH (Fig. 4). Vasquez and Sanchez (1984) reported very similar seasonal patterns for another Orinoco floodplain lake.

By conversion of inorganic macronutrients into biomass, phytoplankton significantly affected the partitioning of macronutrients in the drainage and isolation phases. During this period, the high densities of phytoplankton (Fig. 6), as well as the generally low mass ratio of particulate carbon to nitrogen (mean, 8.3), indicate that most of the particulate carbon and nitrogen was algal biomass (Syrett 1981); microscopic examination of the phytoplankton samples confirms this conclusion. Thus patterns in concentrations of particulate carbon, nitrogen, and phosphorus during the drainage and isolation phases essentially reflect patterns in phytoplankton biomass, until sediments are resuspended in the late isolation phase.

Heterocystous blue-green algae were abundant during periods of nitrogen gain (Fig. 7). An order-of-magnitude estimate of the nitrogen-fixing potential of the heterocystous blue-greens in Lake Tineo was made on the basis of the relationship between heterocyst densities and daily nitrogen fixation in Lake Valencia, Venezuela, which has a similar light regime, transparency, and

plankton composition (Levine and Lewis 1987). For the nitrogen gain between 21 October and 6 January, when nitrogen was measured weekly, the potential nitrogen fixation in Lake Tineo as estimated from heterocyst densities was 1,190 kg of nitrogen. The observed nitrogen gain during this period was 2,770 kg. Thus the nitrogen gain can be accounted for by nitrogen fixation.

We have not provided explanations for several cases in which measured concentrations of variables deviate considerably from the model concentrations. The decrease in sulfate during the drainage and early isolation phases (Fig. 4F) may have been caused by sulfate reduction or by accumulation of sulfur in algal biomass, but there is not sufficient evidence from this study to determine which mechanism is more likely. Similarly, the concentration of calcium decreased throughout the drainage and isolation phases (Fig. 4D). Theoretical calculations show that calcite precipitation would not occur; other possible explanations for the decrease in calcium include assimilation by phytoplankton and ion exchange.

From this study the effects of the seasonally inundated forest on the chemistry of the lake seem unexpectedly small. Nutrient additions to the lake from leaching and decomposition in the floodplain forest would be expected to occur primarily during initial inundation, as has been noted in certain Amazon floodplain lakes (Braun 1952; Junk 1970). However, comparison of observed nutrient concentrations with model concentrations does not show evidence for large releases of nutrients from freshly inundated areas, and occasional sampling in the flooded forest showed nutrient concentrations similar to those of the open-water area. Herbaceous vines and some other forest plants appear to assimilate nutrients directly from the lake water during inundation (Junk 1984), and their effects on nutrient concentrations in this lake could be significant. However, because these plants tend to be restricted to well-lit edges and clearings of the forest, which account for a small proportion of the total area, their effects on nutrient concentrations are probably less important than the effects of phytoplankton and floating grasses.

In general, changes in the chemistry of river water during passage through Lake Tineo were surprisingly small; their magnitude is probably explained largely by the short residence time of river water in the lake during through-flow. Conversion of inorganic nitrogen and phosphorus to organic forms during through-flow is the most significant chemical transformation. Mass-balance data for Lake Tineo show net retention of nitrogen, despite high nitrogen fixation rates. Net retention of N is explained by the sequence of events: major nitrogen fixation is limited to the interval when the lake is isolated from the river. Lake Tineo also retains phosphorus, but shows a net yield of inorganic carbon on an annual basis. Failure of the lake to yield organic carbon is potentially significant in view of the general uncertainty about the net carbon yield from floodplains (Junk 1985).

Although many aspects of the seasonal cycles in Lake Tineo are similar to those reported for floodplain lakes of the Amazon, there are some notable differences. Most of the Amazon lakes that have been studied are always connected with the river and are larger and deeper than Lake Tineo. In these lakes thermal stratification persists at high water and the hypolimnion becomes anoxic (Tundisi et al. 1984), whereas in Lake Tineo, which is shallower and has a shorter hydraulic residence time, anoxic waters were not observed. The water level in the Amazon lakes at low water is determined by the river, rather than by evaporation, and local drainage and rainfall on the lakes appear to be more important to their chemistry because there is a less pronounced dry season in the areas of study (Furch 1984b). The seasonal cycles of macrophyte and phytoplankton populations in Lake Tineo resemble those reported in Amazon lakes.

In comparison with other tropical lakes, floodplain lakes undergo a much broader spectrum of abiotic and biotic change throughout the annual cycle. The depth, area, and volume of floodplain lakes change continually while the lakes are connected with the river. The annual inundation of floodplain lakes by the river flushes their basins and establishes an initial chemical

setpoint. The chemistry of the lake then diverges rapidly from that of the river under the influence of abiotic processes, which include evaporative concentration of the water and resuspension of sediments, and biotic processes, which include macrophyte decomposition and phytoplankton blooms.

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