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## PRIMARY PRODUCTION IN THE ORINOCO RIVER

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*Abstract.* Autotrophic carbon fixation was studied from 1982 to 1985 along a 500-km reach of the Orinoco River, Venezuela, and in three major tributaries (Apure, Caura, Caroni). Among the tributaries, the annual mean gross primary production (measured as carbon) was highest for the Apure River ( $26 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ), a whitewater river that drains from the Llanos region to the north of the Orinoco. Mean annual production was lower in the blackwater tributaries draining from the Guayana Shield to the south (Caura,  $13 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ; Caroni,  $4 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ). In the Orinoco main stem, mean production varied among stations from  $19\text{--}43 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ . Both in the main stem and the tributaries, production per unit volume and per unit area peaked during the period of low water. Seasonal variations at a given station were almost entirely explained by variations in the phytoplankton biomass per unit volume rather than by seasonal variations in transparency. However, differences in mean transparency among the tributaries partly explained differences in mean production per unit area: suppression of potential production by dissolved and suspended substances was 85% in whittwaters (Apure), 40% in blackwaters (Caura, Caroni), and intermediate in the Orinoco main stem.

Autotroph biomass (as chlorophyll *a*) was highest for the Apure River (mean,  $0.36 \mu\text{g/L}$ ), lowest for the blackwater tributaries ( $0.01\text{--}0.04 \mu\text{g/L}$ ), and intermediate for the Orinoco River ( $0.11\text{--}0.19 \mu\text{g/L}$ ). Transport of biomass had a different seasonal pattern than either production per unit area or biomass per unit volume. All stations along the main stem of the Orinoco River and all tributaries except the Caroni, which is impounded by a large dam, showed a significant rise in transport of algal biomass at high discharge, particularly on the declining limb of the hydrograph. Significant transport also occurred during the period of low water, well after the period of contact between the river and the floodplain.

A mass-balance method was used in estimating the yield of phytoplankton biomass from the floodplain to the river. The annual carbon yield per unit floodplain area from  $3660 \text{ km}^2$  of floodplain was only  $75 \text{ mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ , or  $<1\%$  of estimated floodplain phytoplankton production. The data indicate that non-floodplain sources, including within-channel and near-channel stagnant or slow-flowing areas, account for 63% of the annual transport of phytoplankton carbon ( $2.4 \times 10^6 \text{ kg/yr}$ ), while the floodplain accounts for only 37%. The floodplain, although productive, conserves algal production, and in this respect functions as a closed system, even though it is physically an open system.

*Key words:* floodplain–river interaction; mass balance; Orinoco River; river primary production; seasonality in tropic rivers; tropical river phytoplankton; Venezuela.

### INTRODUCTION

Primary production has been studied much less extensively in running waters than in standing waters (Bott 1983). Even so, some general principles are evident from field studies and from the physical constraints on primary producers in running waters. First, it is clear that streams of small to moderate size lacking a tree canopy may support high primary production that is mainly based on attached algae (Minshall 1978). Small streams are easily shaded, however, and thus may have very low primary production in forested areas (Fisher and Likens 1973, Cummins 1974). In large rivers, there is greater likelihood of unstable substrate and of significant extinction of light by the water

over the substrate. These factors tend to reduce primary production by attached algae. At the same time, however, large rivers are less subject to shading, and are likely to receive sufficient irradiance to support rapid photosynthesis near the water surface. Consequently, a shift from attached to suspended primary producers is likely to occur along the gradient from small to large rivers (Minshall et al. 1983).

The greater depth of large rivers may discourage the growth of suspended as well as attached algae if the combination of depths and extinction coefficients is such that the average irradiance reaching individual algal cells nears the threshold for net growth (Vannote et al. 1980). Primary production in large rivers is thus to a large degree controlled by transparency and depth in relation to the photosynthetic capabilities of suspended algae, and may be high or low depending on

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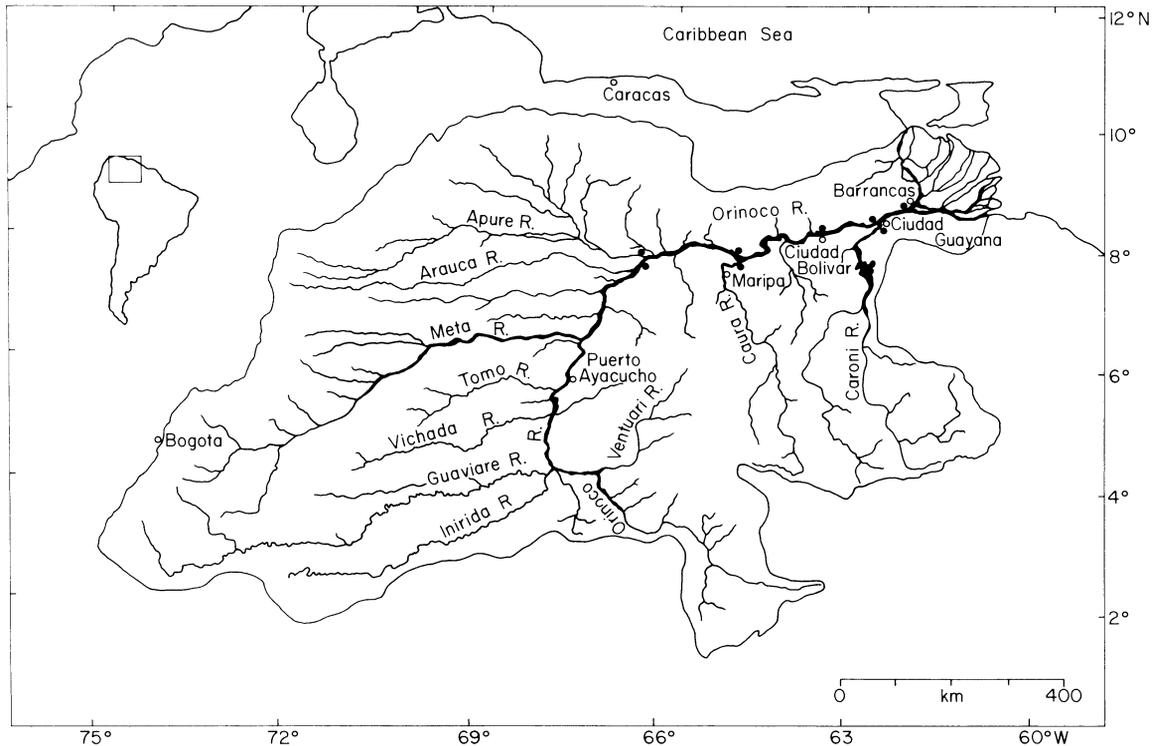


FIG. 1. Map of the Orinoco River drainage showing the river sampling sites.

the combination of these factors. The literature is still too limited in scope to give a general picture of the importance of primary producers in large rivers.

Another factor that controls primary production in large rivers, but is seldom explicitly recognized, is the size of the algal inoculum that the river receives. The inoculum may originate from substrates or from standing waters that are flushed as discharge changes. In particular, the floodplains of large rivers have great potential to govern the size of the inoculum of suspended algae in the river. The influence of river floodplain on the inoculum of algae in the river may have been partially obscured by the tendency of river ecologists to study rivers that flow through populated areas where both the rivers and the floodplains have been strongly regulated.

The present study deals with primary production in the flowing waters of the Orinoco River and of three of its major tributaries: the Apure, the Caura, and the Caroni (Fig. 1). The purpose of the study is to quantify primary production and algal biomass in these flowing waters, to describe the seasonal cycles in these variables, to identify the influence of the floodplain in supplying the inoculum for algal growth, and to test the feasibility of a mass-balance approach for calculating the transport rates of algae from the floodplain to the river. Primary production in the flowing waters of large tropical rivers that have not been extensively altered

is of interest in part because it has not been systematically measured. Furthermore, the information on primary production for the Orinoco River and its major tributaries may indicate some of the interactions between flowing waters and floodplains that are more difficult to identify in the greatly altered rivers of many parts of the world.

#### DESCRIPTION OF THE STUDY AREA

The Orinoco River drains an area of  $1.1 \times 10^6$  km<sup>2</sup> within Venezuela (70%) and Colombia (30%). To the north and west of the watershed, the tributaries of the Orinoco originate in the Andes and the adjoining Cordillera de la Costa. To the north, rivers leaving the Andes flow across alluvial grasslands (the Llanos) for a great distance before reaching the Orinoco River. To the south, tributaries flow through deciduous or evergreen tropical forest (Ewel et al. 1976). In general, there is a trend toward increasing precipitation from north to south. Some of the northern areas of the watershed receive amounts of precipitation as low as 1000 mm/yr, while others to the south receive precipitation in excess of 6000 mm/yr (Ewel et al. 1976).

The Orinoco watershed is geologically diverse. To the south of the Orinoco River is the Guayana Shield, which consists of lithologically complex Precambrian rock (Case et al. 1984). The waters draining from this portion of the watershed are typically very low in elec-

trolytes and often have a strong dark color caused by dissolved organic carbon (Lewis et al. 1986). The waters draining from the north have higher amounts of electrolytes and higher concentrations of suspended solids.

The watershed of the Orinoco River is sparsely inhabited (Zinck 1980). Most of the natural vegetation, particularly to the south, is intact, and development does not appear to have altered the overall characteristics of the natural system in any important way. The one regional exception is the Caroni River, which has been impounded by the Guri Dam. Because the Caroni River is impounded, its natural flow regime has been altered, although its chemistry seems to have been little changed by impoundment (Lewis and Weibezahn 1976).

The fringing floodplain of the lower Orinoco River is relatively narrow (mean, 6 km), and contains many permanent and seasonal lakes (Vasquez 1984, Hamilton and Lewis 1987). The floodplain is separated from the river by a natural levee. River water enters the floodplain through channels in the levee. The floodwaters inundate large amounts of forest as well as open areas. At high water, an area of 6940 km<sup>2</sup> is inundated on the fringing floodplain below the Meta River; at the end of the dry season, the area of standing water in this floodplain is 470 km<sup>2</sup> (S. Hamilton and W. M. Lewis, Jr., *personal observation*).

The floodplain of the Caura River (325 km<sup>2</sup> of water during inundation) resembles that of the lower main stem of the Orinoco River, but is more dominated by forest and has few lakes. In contrast, the floodplain of the Apure River extends far from the river channel and is contiguous with the floodplains of the Meta and other smaller rivers draining from the north side of the Orinoco (Fig. 1). The floodplain of the Apure River forms an internal delta with the adjoining river floodplains. During inundation, standing water in contact with the river covers 4920 km<sup>2</sup> (less than the 70 000 km<sup>2</sup> indicated by Welcomme 1979), although a much larger area becomes very wet because of poor drainage. The internal delta is grassy, open, and flat except for canals and depressions formed by the movement of water.

#### METHODS

The Orinoco River and its major tributaries were studied between 1982 and 1985. Over this 4-yr interval, three stations along the Orinoco main stem were sampled biweekly for the first 2 yr and monthly for the second 2 yr from a field laboratory located at Ciudad Bolivar (Fig. 1). Samples were also taken on the same schedule of the Caroni and Caura rivers, which drain into the Orinoco from the south. For 20 mo, samples were taken of the Apure River, which drains from the north, and of the Orinoco River just above the Apure.

The average time required for water to flow from the headwaters to the mouth of the Orinoco River is  $\approx$ 2 wk. Samples were collected in a downstream direction

on a schedule that corresponded approximately to the travel time of water.

It has been shown that the waters of the Orinoco River are not always horizontally and vertically uniform in chemistry or particulate load, even as much as 100 km below any major tributary (Lewis and Saunders 1984). Although the samples of the Orinoco main stem were in all cases taken as far as possible from any major upstream tributaries, so that the problem of characteristic sampling would be reduced, a flow-integrating sampler was used in taking all of the river samples (Nordin and Skinner 1977, Nordin et al. 1983). The flow-integrating sampler was lowered from top to bottom at 4–5 points along the cross section at each of the river stations on the Orinoco and on the tributaries. In this manner, a composite sample at each station was obtained for primary production, water chemistry, and phytoplankton. A large subsample of the integrated sample was enclosed in a plastic bottle and stored in a dark, cool container in which it was returned to the field laboratory, where measurements of primary production were made. Holding time between collection and incubation varied typically between 2–48 h, with a mode of 12–24 h. Cell counts of individual species conducted on four separate dates showed no significant decline in cell numbers within 48 h.

Primary production was measured in an incubator that was designed to provide a close approximation of the conditions in the river (Fig. 2). The incubator included reservoir containers enclosed in a dark box. Each reservoir container was connected to a length of tubing. There were two types of reservoir/tubing combinations. One type, which was used in light incubations, included transparent tubing that passed through a light gradient. In the second, which was used in dark incubations, the tubing was darkened. For all of the work reported here, both a light and a dark incubation were performed on a portion of each sample.

Connected to each set of tubing was a peristaltic pump. The reservoir was filled with the sample that was to be incubated, after which a known amount of carbon-14 was added and the system was closed. The peristaltic pump was then adjusted to a constant rate of flow to keep the sample moving through the system at sufficient speed to prevent sedimentation. Upon passing through the peristaltic pump, the water entered the tubing system and then returned to the reservoir. During a dark incubation, the cells spent the entire incubation in complete darkness. For a light incubation, any given algal cell spent a portion of its time in complete darkness (in the reservoir), as it would deep in the river, and a portion of its time passing through a light gradient, as it would near the surface of the river. After the samples had been incubated for several hours in the sunlight, the pump was shut off and a portion of the sample was removed for filtration. When not in use, the incubator was stored in the dark after being filled with dilute sulfuric acid in order to prevent

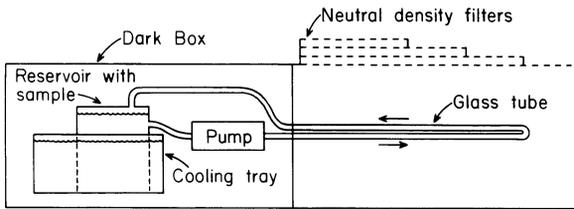


FIG. 2. Diagram of the circulating incubator used in measuring primary production.

the growth of organisms in the containers; the system was flushed with freshwater before its next use.

In all of the incubations, 1.5 MBq of carbon-14 in the form of sodium bicarbonate were added to a 1-L portion of the sample in the reservoir at the time of incubation. The samples were incubated for 4–5 h over the middle of the day. Start and stop times for the incubation were noted, so that the amount of irradiance falling on the incubator could be determined from the records of incident irradiance that were continuously maintained at the field laboratory. The light gradient for light incubations ranged in six increments from 7.9% of incident irradiance to 59.3% of incident irradiance. The pumping rate was adjusted so that the passage time for any given cell through the light gradient would be  $\approx 60$  s. For every 60 s in the light, cells averaged 20 min in the dark reservoir. Because of these brief exposures, it can be assumed that there was no significant light inhibition (Harris 1978). Light exposures of cells within the incubator were within the range of actual light exposures of cells moving randomly within the rivers. However, exact correspondence of incubation conditions with field conditions was not necessary because production in situ was calculated from relative production (production per unit of irradiance) rather than absolute production, as explained below.

Incident irradiance was measured with a pyrheliometer and was then converted to quantum units (moles per square metre per day) of photosynthetically active radiation (PAR, 400–700 nm) on the basis of the expected energy distribution of irradiance (Steemann-Nielsen 1975), as validated in the field with a quantum sensor. The total irradiances on all days of the 4 yr of the study were similarly converted to quantum units to allow estimates of production over intervals between sampling dates.

The concentration of dissolved inorganic carbon, which is essential for the computation of primary production corresponding to a given rate of fixation of carbon-14, was determined as described by Lewis et al. (1987). After each C-14 incubation, duplicate 50-mL portions of water from each reservoir were filtered (pore size 0.45  $\mu\text{m}$ ). Filters were then rinsed thoroughly with river water, placed in a liquid scintillation vial, treated with scintillation cocktail containing a solubilizer, and counted with a liquid scintillation counter.

Each vial was then spiked with a known activity of carbon-14 and recounted. The spike recovery served as the estimate of counting efficiency for each scintillation vial.

Photosynthetic carbon fixation was calculated as described by Lewis (1974). An isotope discrimination factor of 1.06 was used in all of the computations. For a given sample, the activity of the dark incubation was subtracted from the activity of the light incubation. The net activity of the light incubation was then converted to carbon fixed per unit of light for a given station and date. It is assumed for present purposes that carbon fixation computed in this manner corresponds to gross primary production (Harris 1978).

Light exposures of cells in the rivers were computed for each date and station from incident irradiance for the day (with 10% allowance for surface loss) and the amount of light (PAR) at depth increments of 1 cm as derived from the extinction coefficient measured with a quantum sensor in the field. The light exposures in situ at each 1 cm increment of depth were then multiplied by the experimentally determined fixation rate per unit volume per unit of PAR, and fixation was integrated over depth to provide the estimate of production per unit area per day. This procedure assumes that the fixation at a given depth is linearly proportional to PAR at that depth; the proportionality constant is the experimentally determined volumetric fixation per unit of PAR. The assumption of linearity is not a significant source of error given the close correspondence of experimental and field exposures to light and the low intensities of light exposure, which would minimize nonlinearity.

Records of discharge of the Caroni River, which is gauged at the Guri Dam, were obtained directly from the dam authority (Corporacion Venezolana de Guayana). Discharges for the other rivers, including the Orinoco main stem, were more difficult to obtain. Although the Venezuelan government has extensive records of stage height for major rivers within Venezuela, definitive relationships between stage height and discharge have not been established until recently. Within the last 5 yr, the Venezuelan government has undertaken a series of careful measurements in cooperation with the United States Geological Survey. These measurements were used along with the stage height data in constructing curves relating discharge to stage height.

For the Caura River, it was possible to use a single curve to represent the entire range of discharges. For the Apure River, it was necessary to use three different curves to obtain an adequate fit because of the major changes in flow characteristics that occur in the Apure River as the river floods extensive areas beyond its channel at high water. For the Orinoco River, it was necessary to use two equations because of the change in flow characteristics when the Orinoco enters its floodplain. Because valid calibration values for the Ori-

noco River are the most difficult to obtain, only the calibrations that were considered to be the most sound were used (R. Meade, United States Geological Survey, *personal communication*).

Attempts were made to measure chlorophyll *a* (chl *a*) in the river water by standard extraction and spectrophotometric techniques. Except when the chlorophyll concentrations were exceptionally high, spectrophotometric methods proved to be unreliable because of a combination of very low concentrations of chlorophyll, high concentrations of colored organic compounds, and significant amounts of extremely fine particulate material in the water. Although the extinction caused by colored compounds and by particulate material can typically be segregated from chlorophyll absorbance by measurement of absorbance at different wavelengths, realistic estimates were not possible because the interference corrections were not stable.

Because it was not possible to measure chlorophyll *a* directly, a method was developed for indirect estimation of chlorophyll *a*. The efficiency of photosynthesis (fixation per unit of biomass per unit of light) is much more constant than absolute fixation (Harris 1978). This is especially true in nutrient-sufficient populations of phytoplankton photosynthesizing near the linear region of the photosynthesis-light response curve. Phytoplankton in the running waters of the Orinoco River system are consistently nutrient-sufficient, as demonstrated by the presence of substantial amounts of inorganic nutrients in solution. In the main stem, soluble reactive P was consistently in excess of 10  $\mu\text{g/L}$  (mean, 14  $\mu\text{g/L}$ ), and inorganic N was consistently above 50  $\mu\text{g/L}$  (mean, 95  $\mu\text{g/L}$ ). In the Apure, the concentrations were higher; in the blackwater tributaries, the concentrations were somewhat lower (Lewis 1986), but still high in relation to uptake requirements. Maximum potential metabolic requirements of N or P to support observed production was always one-tenth or less of the measured inorganic nutrient supply. Consequently, it should be possible to make an approximate conversion from the photosynthesis per unit volume per unit of irradiance to the chlorophyll upon which this photosynthesis is based.

Platt and Jassby (1976) have shown that most values for efficiency of photosynthesis (as carbon uptake per unit chl *a* per unit quantum flux) fall within the range 7–14  $\text{mg} \cdot \text{mg}^{-1} \cdot \text{mol}^{-1} \cdot \text{m}^{-2}$  (due to a units conversion error, this range is shown incorrectly by Harris (1978) as 2–4  $\text{mg} \cdot \text{mg}^{-1} \cdot \text{mmol}^{-1} \cdot \text{m}^{-2}$ ). For present purposes, we use a midrange value of 11  $\text{mg} \cdot \text{mg}^{-1} \cdot \text{mol}^{-1} \cdot \text{m}^{-2}$ . This estimate is consistent with separate estimates based on  $P_{\text{max}}$  (the maximum rate of photosynthesis) in various kinds of freshwater environments under nutrient-sufficient conditions at the minimum irradiance required to produce  $P_{\text{max}}$ , as computed from Harris (1978).

Subsamples of each sample were preserved with Lugol's iodine solution so that the phytoplankton contributing to primary production could be examined as

desired. When high production was measured, presence of high numbers of algal cells was checked on the preserved samples with an inverted microscope as a means of validating the estimates of production and chlorophyll. Also, on the few occasions when reliable spectrophotometric chlorophyll measurements seemed least affected by methodological problems, the measurements were consistent with the indirect estimates.

## RESULTS

### *Discharges and patterns of floodplain inundation*

The seasonal cycle of discharge was very similar at all of the sampling stations, despite variation in total annual precipitation over different portions of the watershed (Fig. 3, Table 1). On the Caroni River, the presence of the Guri Dam sharpened the seasonal transitions in discharge, and held the minimum discharge at a steady level. At the other stations, discharge changed almost continually. Minimum discharge typically occurred in late March or early April. The date of maxima for a given year coincided very closely among stations, and there was high uniformity in timing of the maxima among years as well. Maxima typically occurred in the last half of August or the first half of September. The dates of minima and maxima for the Caroni, because of the dam, were more variable.

The discharges at all sites were greater during the first 2 yr of the study than during the last 2 yr, but the range of variation across years was relatively small (Table 1). The ratio between maximum and minimum discharge was highest for the Apure River (20–30) and lowest for the Orinoco and Caura rivers (10–20). The discharge of the Orinoco River as shown in Table 1 is considerably higher than a number of estimates reported in the literature (e.g., Czaya 1981, Serruya and Pollinger 1983) because of previous unavailability of reliable calibrations, but is consistent with more recent estimates (36 000  $\text{m}^3/\text{s}$ : Meade et al. 1983).

For both the Orinoco and its tributaries, it is possible to relate discharge to the contact of the river with the floodplain. Detailed observations during 1984 on the floodplain of the Orinoco main stem in the vicinity of Ciudad Bolivar showed that the river first entered the floodplain at a discharge of  $\approx 37\,100\ \text{m}^3/\text{s}$ , and that the last floodplain waters drained into the river at a discharge of approximately 32 100  $\text{m}^3/\text{s}$  (Hamilton 1985). During 1984, these discharges corresponded to the interval 1 July–30 December, or 148 d. The period of contact with the floodplain was divided into three phases. From 1 July to 30 July (37 100–43 400  $\text{m}^3/\text{s}$ ), floodwaters were penetrating the floodplain but not flushing it. Between 30 July and 4 November (43 400–39 800  $\text{m}^3/\text{s}$ ), the floodwaters were flushing the floodplain. Between 4 November and 30 December (39 800–32 100  $\text{m}^3/\text{s}$ ), the floodwaters were draining from the floodplain. In wetter years, such as 1982, the period of contact between the river and the floodplain lasted

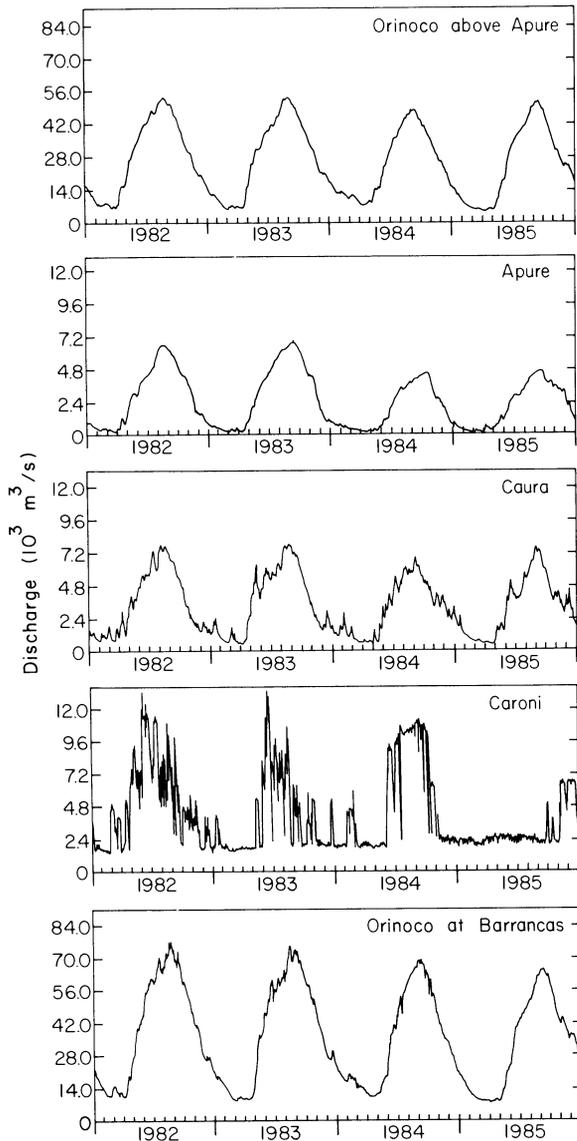


FIG. 3. Discharge of the Orinoco River and the three tributaries at the sampling stations over the 4-yr study interval.

close to 180 d, mainly because of extension of the throughflow and drainage phases associated with an earlier beginning of the rise in discharge. The Caura River entered its floodplain at a discharge of  $4350 \text{ m}^3/\text{s}$ , and the Apure entered its floodplain at a discharge of  $3450 \text{ m}^3/\text{s}$ . The duration of the flooding phase for these two rivers was very similar to the duration of the flooding phase along the lower Orinoco.

#### Primary production and biomass

Figs. 4 and 5 show the pattern of primary production at all of the sampling stations over the entire sampling period. Production was accounted for at all stations by a wide mixture of suspended algae. Dominant taxa included the diatoms *Melosira* and *Rhizosolenia*, fla-

gellates such as *Chlamydomonas* and *Cryptomonas*, and coccoid or filamentous blue-green algae.

For the Apure River, primary production was much higher during the period of low water than at any other time of year. The single highest production rate coincided with the minimum discharge for the year of sampling. The seasonal rise in production began well before the Apure River had reached its minimum discharge, and was thus shifted within the period of low flow toward the phase of falling water; the peak did not extend significantly into the interval of rising water.

For the Caura River, there was also a strong low-water peak in production that was shifted toward the period of declining discharge. The maximum production typically occurred 2–4 wk prior to the date of minimum discharge. The timing of the peaks was essentially the same in all three of the low-water seasons covered by the data base. However, the maximum production was much higher in 1984 than it was in 1985 or 1983. The high value for 1984 was confirmed by examination of the sample from that date, which contained exceptionally large numbers of phytoflagellates (*Chlamydomonas*), Chlorococcales (*Dictyosphaerium*), and diatoms (*Eunotia*). It is likely that the sampling coincided with a brief pulse of phytoplankton abundance in the river caused by the flushing of a large river pool or side channel. Flushing of this type during low water is also apparent from zooplankton data for the Caura River (Saunders and Lewis 1987a).

Primary production in the Caroni River is affected by the Guri Reservoir. Even so, there was a peak in production during the interval of low discharge, as in the other rivers. For the Caroni River, however, the

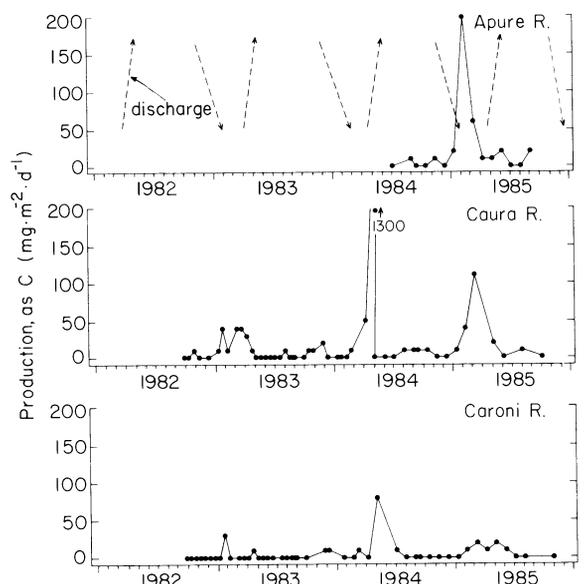


FIG. 4. Primary production per unit area at the sampling stations on the three major tributaries over the sampling interval.

TABLE 1. Summary of discharge data over the four study years.

Station	Discharge (m <sup>3</sup> /s)				Date of minimum	Date of maximum
	Mean	%*	Min	Max		
1982						
Orinoco above Apure	28012	71	6178	53575	21 Mar	24 Aug
Apure Mouth	2871	7	269	6572	28 Mar	18 Aug
Orinoco above Caura	30882	79	6484	60086	21 Mar	24 Aug
Caura Mouth	3508	9	767	7832	17 Mar	6 Aug
Orinoco at Ciudad Bolivar	34390	87	8046	67562	21 Mar	23 Aug
Caroni Mouth	4923	13	1316	13356	20 Feb	4 Jun
Orinoco at Barrancas	39313		10231	77389	2 Apr	21 Aug
1983						
Orinoco above Apure	27444	73	5484	53489	3 Mar	4 Sep
Apure Mouth	2990	8	197	6907	8 Apr	12 Sep
Orinoco above Caura	30434	80	5770	60102	3 Mar	4 Sep
Caura Mouth	3603	10	504	7790	6 Apr	26 Aug
Orinoco at Ciudad Bolivar	34036	90	7190	67477	22 Feb	31 Aug
Caroni Mouth	3797	10	1434	13356	15 Feb	16 Jun
Orinoco at Barrancas	37833		8749	75422	27 Feb	15 Aug
1984						
Orinoco above Apure	24763	72	7369	48031	3 Apr	31 Aug
Apure Mouth	1840	5	200	4465	15 Apr	14 Oct
Orinoco above Caura	26602	77	7616	51901	10 Apr	11 Sep
Caura Mouth	3016	9	357	6759	30 Apr	5 Sep
Orinoco at Ciudad Bolivar	29618	86	8236	58257	10 Apr	7 Sep
Caroni Mouth	4897	14	1518	11176	21 Apr	11 Sep
Orinoco at Barrancas	34515		10165	69201	11 Apr	4 Sep
1985						
Orinoco above Apure	24106	76	4492	51396	6 Apr	14 Sep
Apure Mouth	1983	6	113	4523	31 Mar	21 Sep
Orinoco above Caura	26094	82	5052	55908	2 Apr	14 Sep
Caura Mouth	3062	10	413	7476	23 Apr	2 Sep
Orinoco at Ciudad Bolivar	29094	91	5636	62972	2 Apr	14 Sep
Caroni Mouth	2742	9	1610	6593	2 Jan	15 Oct
Orinoco at Barrancas	31827		7466	65085	2 Apr	13 Sep
1982-1985 (means)						
Orinoco above Apure	26081	73	5881	51623	24 Mar	3 Sep
Apure Mouth	2421	7	195	5617	5 Apr	16 Sep
Orinoco above Caura	28503	79	6231	56999	25 Mar	6 Sep
Caura Mouth	3297	9	510	7464	11 Apr	25 Aug
Orinoco at Ciudad Bolivar	31785	89	7277	64067	22 Mar	3 Sep
Caroni Mouth	4090	11	1470	11120	22 Feb	12 Aug
Orinoco at Barrancas	35872		9153	71774	27 Mar	29 Aug

\* Percent of the discharge at Barrancas.

size of the peak was generally lower and the peak was shifted toward the period of rising water rather than toward the period of falling water.

On the Orinoco main stem, the four stations that were sampled all showed essentially the same pattern as the tributaries; the peak of production fell within the interval of low water, and was shifted toward the period of declining discharge. For the main stem, the peak for primary production was broader than it was for the tributaries. Although the peak of primary production coincided with low water for the Orinoco main stem and the tributaries, there was also typically a small rise in primary production near the time of peak discharge.

The production per unit area on any given date is affected by the transparency of the water, the amount of incident irradiance, and the relative production (pro-

duction per unit volume per unit irradiance). However, for all stations the pattern of relative production and biomass were essentially identical to the pattern of production per unit area. Spearman rank correlation coefficients between production per unit area and relative production or biomass exceeded 0.90 ( $P < .01$ ) for all stations and exceeded 0.95 for all stations except the Orinoco above the Apure. For this reason, it is redundant to present the data for relative production or biomass in graphical form.

As shown by Table 2, relative production and algal biomass were highest for the Apure River and lowest for the Caroni and Caura rivers. The mean values for relative production and biomass along the Orinoco main stem were between the extremes for the tributaries. Most of the maxima for relative production and biomass were 3-7 times the mean.

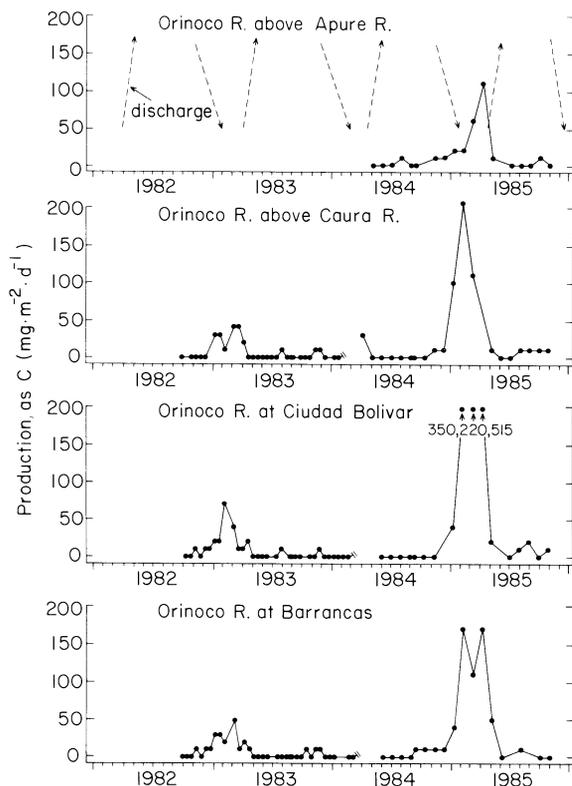


FIG. 5. Primary production per unit area at the four sampling stations on the Orinoco main stem over the sampling interval.

The station ranks for production per unit area were somewhat different than the station ranks for relative production and biomass. The production per unit area of the Apure River was within the midrange of main-stem values rather than above the main-stem values, as was the case for relative production. The rates of production per unit area of the Caroni River and of the Caura River were much higher in relation to the

other values in the series than might have been expected on the basis of relative production. The shifts in rank between relative production and production per unit area are explained by differences in transparency. Higher relative production in the Apure River was partially offset by lower transparency, and the reverse was true for the Caura and Caroni rivers, which were more transparent than the Apure. Thus although relative production and production per unit area were strongly correlated at a given station, mean differences in transparency across stations greatly influenced the differences in mean magnitude of production per unit area among stations.

#### *Inorganic carbon and transparency*

The concentrations of inorganic carbon were highest for the Apure River, lowest for the Caura and Caroni rivers, and intermediate for stations along the main stem of the Orinoco River (Table 3). Concentrations of inorganic carbon were low, but could not have been so low as to suppress algal growth because of the low carbon demand associated with the low levels of primary production shown in Table 2.

Transparencies of the Caura and Caroni rivers were several times as great as the transparency of the Apure River. The lower transparency of the Apure River was associated with a much heavier load of suspended inorganic material. On the main stem, there was high consistency among stations upstream of the Caroni River. However, there was a notable increase in transparency near Barrancas. This downstream increase, which was consistent among years, was probably caused by broadening of the river near the delta and consequent deposition of part of the suspended load.

Large seasonal variations in transparency were characteristic of all stations (Figs. 6 and 7). As might be expected because of impoundment, the range of variation was lowest (twofold) for the Caroni River. For other stations, seasonal variation was between four-

TABLE 2. Mean and maximum values of relative production (production per unit of irradiance), primary production per unit area, and algal biomass (as chlorophyll *a*) at the sampling stations.\* Minima are not given because they were all close to zero.

Station	Relative biomass carbon production ( $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{mol}^{-1}\cdot\text{m}^{-2}$ )		Biomass carbon production ( $\text{mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ )		Chlorophyll <i>a</i> ( $\mu\text{g}/\text{L}$ )	
	Mean	Maximum	Mean	Maximum	Mean	Maximum
Apure Mouth†	3.91	14.16	26.2	198.3	0.355	1.288
Caura Mouth	0.48	2.50	13.2	107.6	0.044	0.227
Caroni Mouth	0.13	0.86	4.11	29.5	0.012	0.078
Orinoco above Apure†	1.34	3.63	18.7	107.0	0.122	0.330
Orinoco above Caura	1.55	8.65	20.5	227.5	0.141	0.787
Orinoco at Ciudad Bolivar	2.08	16.6	42.7	515.6	0.189	1.510
Orinoco at Barrancas	1.19	5.63	23.0	168.5	0.108	0.512

\* Because of the missing data for the period of peak production on the Orinoco main stem during 1984, the year 1984 is excluded for all stations in order to facilitate comparison among stations.

† Only 1 yr of data for these stations.

TABLE 3. Summary of dissolved inorganic carbon concentration, transparency (depth of penetration of 1% surface irradiance), and transport of algal biomass at the sampling stations.

Station	Inorganic carbon (mean, mg/L)	Depth of 1% light (mean, m)	Chl transport (mg/s)		
			Mean	Min	Max
Apure Mouth*	12.95	0.46	436	85	1313
Caura Mouth	0.94	2.63	78	3	202
Caroni Mouth	0.42	2.88	33	0	124
Orinoco above Apure*	1.73	0.95	1836	715	4053
Orinoco above Caura	2.28	0.93	2074	336	7071
Orinoco at Ciudad Bolivar	2.18	0.91	2662	373	9043
Orinoco at Barrancas	1.98	1.23	2117	608	5375

\* Only 1 yr of data for these stations.

and eightfold. All stations had maximum transparency during the period of low water. At most stations there was a sharp increase in transparency as the water levels reached their seasonal minima, followed by an equally sharp decline as the water level began to rise. Minimum transparency was consistently associated with the phase of most rapidly rising discharge. Typically there was a substantial increase in transparency as discharge reached its peak, when the rate of change in discharge was low.

#### Transport of biomass

The transport of algal biomass at any station can be calculated as the product of biomass and discharge. Transport, for which biomass will here be expressed as mass of chlorophyll *a*, is the single most useful variable for interpreting the interaction of the river and its floodplain. Transport does not necessarily vary according to the same pattern as biomass or production per unit area because of the vast seasonal changes in discharge, which can enhance transport greatly even while diluting biomass and thus suppressing production per unit area.

Except for the Caroni, which is affected by the reservoir, the stations share two general tendencies in the time sequence of transport: (1) a pronounced minimum just as discharge begins to rise, and (2) a strong maximum at high water (typically on the declining limb of the hydrograph) (Figs. 8 and 9). On the Apure River, there was a steep rise in transport during the period of rising water. This was succeeded by a drop in transport and then a subsequent rise coinciding with the peak of discharge. There was a third rise during the period of falling water. A similar pattern has been observed for the transport of zooplankton by the Apure River, and probably corresponds to stages of contact between the river and the large adjoining internal delta (Saunders and Lewis 1987*b*). For the Caura River, transport showed only a moderate increase during the interval of low water when biomass per unit volume and production per unit area were at their peak. The maximum transport occurred much later, beginning about the time of peak discharge and extending well into the interval of declining discharge. For the Caroni River, the rise in transport coincided with the rise in water level, and

declined after the peak of discharge. On the main stem of the Orinoco River, the pattern of transport was most similar to that of the Caura River.

As would be expected from the relative discharges and biomass levels, transport was considerably higher for the Apure River than for the Caura or Caroni rivers (Table 3). Along the main stem of the Orinoco River, the annual averages were similar among stations.

## DISCUSSION

### Magnitude of production

The mean biomass and production for the Orinoco main stem and the three tributaries are low by comparison with the values that are commonly encountered in standing freshwaters. Even the maximum con-

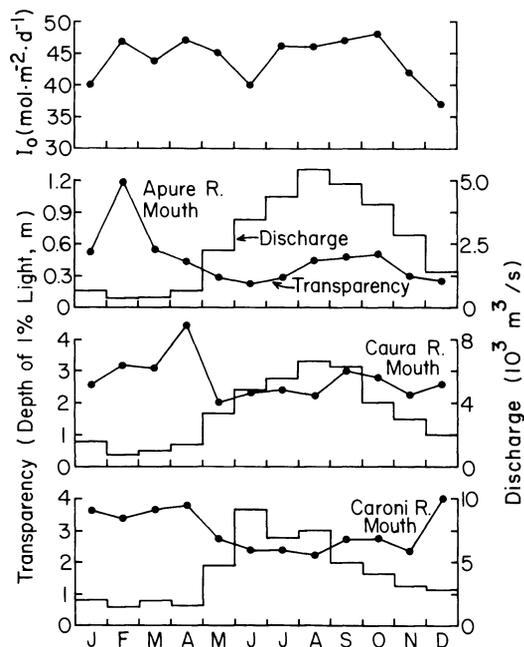


FIG. 6. Incident irradiance ( $I_0$ ) at the Ciudad Bolivar station averaged by month over the sampling interval, and transparency and discharge at the sampling stations on the three Orinoco tributaries averaged on a monthly basis over all years of sampling except 1984.

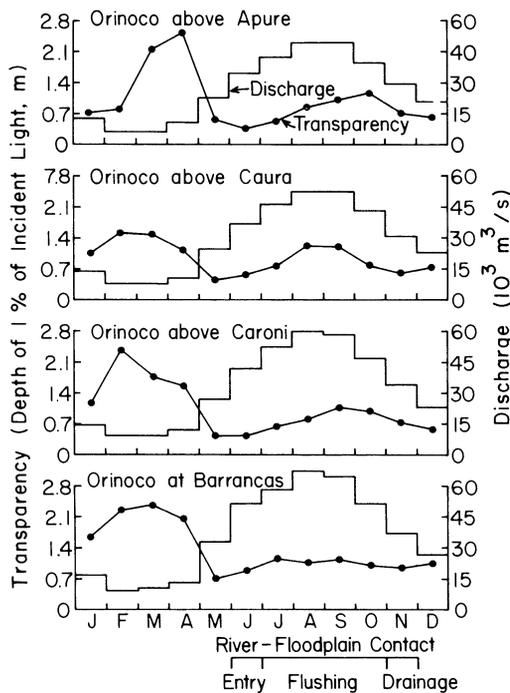


FIG. 7. Transparency and discharge at the four stations along the Orinoco River main stem averaged on a monthly basis for all years except 1984.

centrations of chlorophyll and production per unit area are within the range of values typical of oligotrophic lakes (Welch 1980). Rates of production in the Orinoco and its tributaries are also far below most of the rates that have been measured in the sluggish and often polluted rivers where production has been best documented (Wetzel 1975). Because of the low production rates, autotrophy cannot have an important influence on nutrient concentrations or carbon balance in the flowing waters of high order within the Orinoco system. Seasonal patterns and rates of transport are nevertheless significant as indicators of the events that occur in the floodplain and side channels, where the densities and metabolic rates of algae are generally much higher than in the rivers (Hamilton and Lewis 1987).

Low production in the rivers is only partly explained by low concentrations of algal biomass. Poor transparency of the river waters contributes significantly to the suppression of production, and the degree of suppression by this mechanism differs among the river stations. The degree of suppression can be estimated from a recalculation of production given the hypothetical assumption that there is no extinction of light within the water column by either particulate matter or dissolved organic material, but only by water itself (extinction coefficient for PAR  $\approx 0.1 \text{ m}^{-1}$ ). The relative suppression of production by extinction of light associated with particulate material and dissolved organic matter is greatest for the Apure, least for the Caura

and Caroni, and intermediate for the Orinoco main stem (Fig. 10).

Although suppression of production by low transparency is substantial throughout the lower Orinoco system, production would be low in absolute terms even without this suppression. The proximate explanation for low production, independent of transparency, is low algal biomass per unit volume of water. Underlying low algal biomass are three factors: (1) a small inoculum, which would require a lengthy period of growth before reaching high abundances, (2) high velocities of flow, which reduce the potential for accumulation of biomass in transit, and (3) a deep water column, which severely limits the average light exposure of individual cells, even under conditions of maximum transparency. Of these three factors only inoculum size is not a direct result of the simple physical characteristics of the river. Inoculum size is controlled by the sources of algae, and by seasonal variations in the connection of these sources to the river.

#### Sources of algae

At all stations there were substantial peaks in the density of phytoplankton and in the primary production per unit area during the period of low water. This is probably a widespread feature of tropical rivers (e.g., Iltis 1982). In the Orinoco system, these peaks cannot be explained by the export of algae from the floodplain because the rivers are not in contact with the floodplain at this time. Consequently, the peaks must be explained by events occurring in the river channels. A detailed study of the Caura River showed that peaks in zooplankton abundance during the dry season were associated with the flushing of pools and slow-moving secondary channels connected to the main channel (Saunders and Lewis 1987a). On an absolute scale,

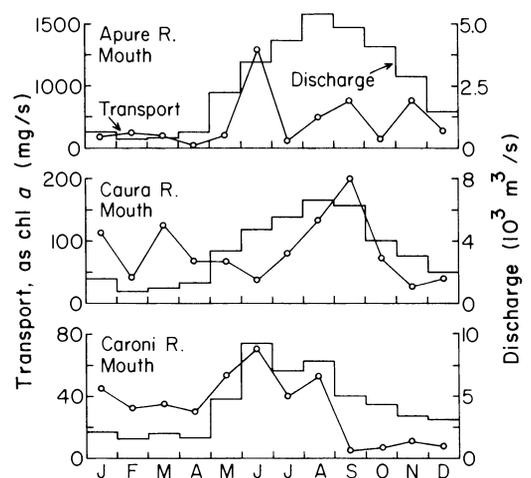


FIG. 8. Transport of algal biomass (as mass of chlorophyll *a*) in relation to discharge for the sampling stations on the three major tributaries averaged over monthly intervals for all years except 1984.

changes in discharge at this time of year are small (Fig. 3), but they are sufficient to cause major changes in the flushing of stagnant areas lying within the channel itself. The stagnant areas accumulate biomass rapidly, and this biomass is subsequently transferred to the flowing portion of the river when a slight change in the river level occurs.

Events in the uppermost portions of the watershed may also help explain the peaks in density and production per unit area of phytoplankton during the interval of low water. Significant growth in the flowing water is most likely during the interval of low flow because of higher transparency, lower average depth, and slower transport at this time. Even at low water, significant net growth of algae cannot occur as far down the river as the sampling stations because of low average light exposures in the deep channel, but significant net growth may be occurring in the shallower water upstream.

During the interval of high water, sources of algae may be different, especially when the floodplain is open to the river. On the Caroni River, transport at high water represents principally the flushing of algae that have grown in the Guri Reservoir. This explains the parallel rise of transport and discharge. The decline of algal transport prior to the decline in discharge is caused by depletion of the accumulated algal biomass in the upper water column of the lake. The pattern of transport for the Caroni River is thus largely artificial and would not be expected in other rivers draining from the Guayana Shield. In contrast, the Caura River shows little transport during the period of rising water, when water is entering the floodplain, because standing waters

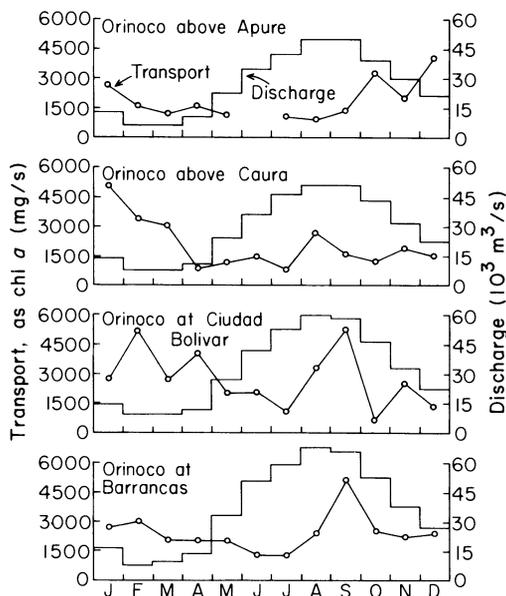


FIG. 9. Transport of algal biomass (as mass of chlorophyll *a*) in relation to discharge for the main-stem stations averaged by month over the study interval excluding 1984.

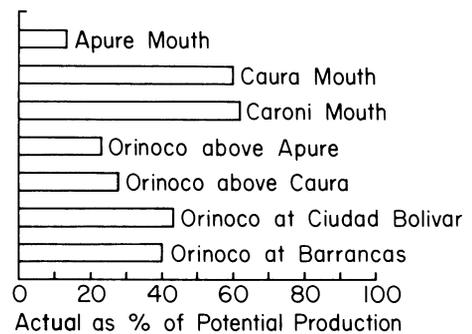


FIG. 10. Suppression of primary production per unit area by the extinction of light caused by dissolved and particulate substances at all sampling stations, relative to the production that would be possible if the only light extinction in the water column was that due to the water itself.

in or near the channel have already been flushed. After the floodplain has filled, and after a refractory interval during which algal growth occurs and flushing rates decline in the floodplain, transport of algae from the floodplain increases. This explains the shift in maximum river transport of algae toward the phase of declining discharge, which coincides with floodplain drainage.

In the Apure River, a rise of phytoplankton transport coincident with the first 2 or 3 mo of rising water probably is explained by the flushing of stagnant environments in or very close to the river channel, and possibly with some contribution from significant growth of algae in the slowly flowing water of the channel itself. Flushing during the period of rising discharge is a larger source of transport on the Apure, probably because of more extensive stagnant water near the channel and because of richer nutrient supplies, which would support much higher standing stock in stagnant areas. After a refractory interval as the water enters the extensive sheet floodplain, growth of algae in the floodplain is reflected in a second increase of transport that coincides with maximum discharge. Transport continues to be high, although variable, as the large floodplain drains back into the main channel of the river.

As would be expected, the patterns of transport in the Orinoco River main stem are a hybrid of the patterns in the Caura and Apure rivers. Transport typically remains well above the annual minimum during the interval of low water. Because the Orinoco is not in contact with its floodplain at this time, transport must be the result of irregular flushing of phytoplankton from sources within the channel, as described for the Caura and Apure rivers. Transport is minimal during the period of increasing discharge because most of the phytoplankton sources in or very near the river channel have been flushed, and floodplain populations are not yet entering the river. During June or July, the Orinoco enters its fringing floodplain, and flushing of the floodplain begins  $\approx$  3–4 wk later. Increases in trans-

port do not occur until August, following a lag corresponding to the development of significant phytoplankton populations in the floodplain. The rate at which algae enter the river from the floodplain is governed by an interaction of flushing rate, which peaks as river discharge peaks, and phytoplankton densities, which approach their annual peaks as the floodplain drains (Hamilton and Lewis 1987).

#### *Rates of transport*

By integrating through time the transport of algae past individual points along the Orinoco River main stem, and adding allowances for the major tributaries, it should be possible to estimate the contribution per running kilometre of floodplain along the river and the yield per unit area of algae from the floodplain over the course of the year. This is basically a mass-balance approach applied to biomass. The estimates must be made across matched data sets, and will be most precise if they are made over great distances rather than between stations that are relatively close together.

The mass-balance approach is simplified for the Orinoco by negligible mortality and growth of algae during transport. Maximum potential growth in transit can be calculated from the production measurements, river transparency, and river depth. For example, the mean chlorophyll concentration of the main-stem stations ( $0.14 \mu\text{g/L}$ ) corresponds to an algal carbon concentration of  $5 \mu\text{g/L}$ , or  $125 \text{ mg/m}^2$  for a river cross section midway along the hydrograph. Mean gross production of biomass C is  $25 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ . Daily respiratory carbon demands for an algal population with a carbon content of  $125 \text{ mg/m}^2$ , based on an oxygen uptake rate of  $1 \text{ mg}$  per milligram of chlorophyll *a* per hour (Harris 1978), would be  $30 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ . Thus net production would be zero; growth could not occur in the river. Calculations of this type for individual dates and individual sites consistently show that gross production does not exceed respiration because of the limited amount of light reaching cells suspended in the river. These conclusions are verified empirically by failure of the phytoplankton populations of the Orinoco main stem to show downstream increases in abundance during the dry season when no phytoplankton sources are available below the tributaries.

Several lines of evidence also show that phytoplankton mortality in the river is negligible over the time required for the river to move between stations (1–3 d, depending on season). No significant grazing mortality is expected over the interval of transport because planktonic grazers are present at very low abundances ( $< 10$  individuals/L; Lundberg et al. 1987) and because benthic filter feeders are virtually absent as a result of the fine substrate and high velocities. Phytoplankton populations held in river water in the dark or in low illumination for 24–48 h are stable, as shown by microscope counts. In addition, it is possible to estimate mortality by use of the data for months when the river

is not in contact with the floodplain. If mortality is negligible, transport at downstream stations should equal transport at upstream stations after addition of transport from the intervening tributaries. If mortality is significant, transport at downstream stations will be less. For the period of no floodplain contact, the data show no significant downstream change in transport. The assumption of negligible mortality in transit thus appears to be sound.

For the flooding period, two sets of mass-balance calculations are possible. In the first set of calculations, transport past the Orinoco above the Caura can be compared with transport past the Orinoco at Barrancas for the entire interval of study except for 1984, which must be eliminated because of missing data. The transport computations are made only for the intervals when algae can enter the main stem from the floodplain. Over this interval (150 d) the average transport is  $1591 \text{ mg/s}$  for the Orinoco just above the Caura River,  $96 \text{ mg/s}$  for the Caura River, and  $33 \text{ mg/s}$  for the Caroni River. Thus the total at Barrancas, without any addition from the floodplain between the Caura River and Barrancas, would be  $1720 \text{ mg/s}$ . The observed transport at Barrancas is  $2060 \text{ mg/s}$ , indicating that  $340 \text{ mg/s}$  of chlorophyll *a* entered the river from the floodplain between the Caura River and Barrancas. Allowing 1% as the amount of chlorophyll in algal dry mass (Parsons et al. 1984) and 36% as the amount of carbon for algal dry mass (Stumm and Morgan 1981), the floodplain yield (as algal carbon) corresponds to  $160\,000 \text{ kg/yr}$  between the Caura River and Barrancas. This is equivalent to  $440 \text{ kg/km}$  of river. The area of the floodplain over this reach of river is  $1965 \text{ km}^2$ ; the annual yield of algal carbon per unit area of floodplain would thus be  $81 \text{ mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ .

A second calculation can be based on a comparison between the Orinoco just above the Apure River and the Orinoco at Barrancas. This comparison covers the floodplain contact interval for only one year (1985) because data are not available for other years at the uppermost station. For 1985, the transport of chlorophyll *a* by the Orinoco just above the Apure was  $1488 \text{ mg/s}$ . To this is added the transport for the other rivers below: Apure,  $634 \text{ mg/s}$ ; Caroni,  $28 \text{ mg/s}$ ; Caura,  $139 \text{ mg/s}$ . Thus the total for the studied river reaches is  $2289 \text{ mg/s}$ . This is compared with the transport at Barrancas over the same interval,  $2823 \text{ mg/s}$ . This difference,  $534 \text{ mg/s}$ , is attributed to the floodplain between these two points. This is equivalent to  $250\,000 \text{ kg/yr}$  as algal biomass carbon, or  $450 \text{ kg}$  per running kilometre of the Orinoco River between the Apure River and Barrancas. The floodplain area over this reach is  $3660 \text{ km}^2$ . The floodplain thus yields  $68 \text{ mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  of algal biomass carbon to the river. Although this estimate overlaps in its data base with the other estimate, the two estimates deal with differing reaches of the river and differing intervals of time. The two estimates agree well, given the possibilities for

variation along the river and among different time intervals. The average of the two can be used as a final composite carbon transport estimate:  $75 \text{ mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ .

The net yield from the floodplain to the river in the form of the carbon in living algal biomass ( $75 \text{ mg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) is surprisingly small in view of the high plankton production of floodplain waters. High phytoplankton abundances in the floodplain ( $0.5\text{--}1.0 \times 10^6$  cells/mL; carbon  $10\text{--}20 \text{ g/m}^2$ ) and substantial supersaturation of the water with oxygen following peak discharge can only be explained by high phytoplankton production (Hamilton and Lewis 1987). Although the phytoplankton production of the floodplain has not been measured directly, the oxygen concentrations and cell counts indicate that production of biomass C exceeds  $1000 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  much of the year. Even though as much as 80% of the floodplain may be shaded by forest and macrophyte mats at high water, the average production would still reach  $200 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ , while the carbon yield of algae from the floodplain is only  $75 \text{ mg/m}^2$  over the 150-d period of contact with the river, or  $0.4 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ . Thus the floodplain yields <1% of its phytoplankton production to the river in the form of living algae.

Two factors can account for low yield of phytoplankton from the floodplain to the river. First, the period of maximum phytoplankton growth overlaps only partially with the interval of contact between the floodplain and the river. During the initial phase of inundation, dilution and flushing rates are so high that phytoplankton biomass cannot accumulate. Only during the last half of inundation, when water levels are falling, does phytoplankton biomass begin to reach the highest levels. Even though this factor reduces export of phytoplankton, it cannot fully explain the very low yields of phytoplankton to the river. In addition, the data indicate efficient harvesting or conversion of phytoplankton biomass en route from the sites of production to the river.

The yield of phytoplankton to the river can also be compared to production in the river. For the Orinoco main stem, annual gross production of biomass carbon per unit of river surface area averages close to  $9.5 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ , as compared with  $0.25 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  added from the floodplain. Thus the addition is relatively small, even in relation to the low levels of river carbon fixation.

### Conclusions

Floodplains have proven difficult to study in a quantitative manner because they are spatially complex, very large, and typically have high flux rates because of the throughflow. The Orinoco study illustrates the possibility of studying floodplain–river interactions by mass-balance methods across long reaches of river and large areas of floodplain. While such studies cannot resolve the mechanisms at work inside floodplains, they can lead to estimates of fluxes that would not be pos-

sible from direct studies of the floodplains. The application of this approach to the Orinoco floodplain leads to two unexpected conclusions concerning phytoplankton. First, it is clear that most of the phytoplankton biomass in the river originates not from the floodplain but from within-channel or near-channel sources. The transport of algae through the river is often as high when the river is out of contact with the floodplain as when the floodplain is draining into the river. If the yield of the floodplain over the floodplain area that was studied ( $3660 \text{ km}^2$ ) is even approximately typical of the floodplain from the delta to the Meta ( $11860 \text{ km}^2$ ), then less than half ( $890000 \text{ kg/yr}$  of algae, measured as carbon, or 37%; possibly somewhat more if floodplains above the Meta were taken into account) of the total annual transport ( $2.40 \times 10^6 \text{ kg/yr}$ ) comes from the floodplain. In fact,  $1.4 \times 10^6 \text{ kg/yr}$  (58%) of the annual algal carbon transport occurs during the dry season, when there is no contact of the floodplain with the river.

A complementary conclusion is that the floodplain, although highly productive of algae, yields only a small fraction (<1%) of its production to the river, despite the large flow of water through the floodplain. Thus the floodplain, while physically an open system, functions very nearly as a closed system with respect to phytoplankton production.

### ACKNOWLEDGMENTS

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