
THE ORINOCO RIVER AS AN ECOLOGICAL SYSTEM

WILLIAM M. LEWIS, Jr., FRANZ H. WEIBEZAHN,
JAMES F. SAUNDERS, III and STEPHEN K. HAMILTON

The ecosystem concept has numerous roots (McIntosh 1985), but probably its clearest early appearance was in an essay by Stephen Forbes entitled, "The Lake as a Microcosm," which was published in 1887. Forbes made the argument that a lake is a functional unit of nature in much the same sense that an organism is a functional unit of nature. Forbes was defining an ecosystem, although this term was not coined until almost 40 years later. Forbes portrayed the lake microcosm (ecosystem) as such a tightly integrated unit that it would be impossible or counterproductive to attempt to analyze by summing up the properties of its parts. Forbes made a

persuasive case for the necessity of a special kind of holistic thinking, which we could now call ecosystem thinking, derived from a superorganismic concept of the ecosystem.

The term "ecosystem" was introduced by Tansley in 1935. Tansley used the term in the broadest possible way to include virtually any combination of organisms and surrounding abiotic environment. Tansley's broad usage allowed natural units of virtually any geographic scope, from a pond to a biome, to be termed ecosystems. Obviously, the degree of functional integration across geographic units as large as a biome is relatively small. Tansley's concept therefore was much looser than that

of Forbes, for whom the central theme was integration of function.

Today the ecosystem concept is often used very loosely, much in the manner of Tansley. However, when the term is used operationally or in a formal sense, it typically corresponds to a functionally integrated unit rather than a block of landscape. Therefore, it seems that our present concept of the ecosystem is closer to that of Forbes than to that of Tansley, even though we may retain looseness in usage for purposes of convenience whenever ecosystem boundaries are not clear. The concept of the ecosystem as a tightly functioning unit was probably reinforced in an important way by Odum's early textbook (1953),

/ **KEY WORDS:** Orinoco River / ecosystem / nutrient cycling /

William M. Lewis, Jr. is Professor of Biology and Director of the Center for Limnology at the University of Colorado, Boulder. Professor Lewis received his doctoral training at Indiana University and has worked on tropical freshwater ecosystems since 1970. Since 1981, he has been a co-director of the joint Venezuelan-North American study of the Orinoco River conducted by the Universidad Simón Bolívar, the University of Colorado, and the Ministerio del Ambiente de los Recursos Naturales Renovables. Address: 122 Ramaley, Campus Box 334, Boulder Colorado 80309-0334, U.S.A.

Franz H. Weibezahn is Professor Emeritus of the Universidad Central de Venezuela and Consulting Professor for the Universidad Simón Bolívar. Professor Weibezahn has long-term research associations with the Orinoco River and is presently directing research on the Guri Reservoir.

James F. Saunders, III is Associate Director of the Center for Limnology at the University of Colorado and obtained his doctoral degree from the University of Colorado. He has worked on tropical freshwater ecosystems since 1976, primarily in Venezuela, with emphasis on aquatic food chains and biogeochemistry.

Stephen K. Hamilton obtained a Master's degree from the University of Colorado in 1985 and is presently enrolled in the doctoral program at the University of California, Santa Barbara. He has worked extensively on the Orinoco floodplain and also has field experience in the Amazon.

which used a lake in defining an ecosystem (McIntosh 1985).

Forbes not only introduced ecosystem thinking, but also specified some organizing principles that could be applied to the study of ecosystems. He identified food chains and biotic competition for food as organizing principles, and noted that spatial organization is forced on the biological component of an ecosystem by its physical characteristics. He identified the significance of the circulation of matter in lakes, and in this way anticipated the modern concepts of mass balance and nutrient cycling. He also recognized the equilibrium between synthesis and breakdown of organic matter inside the system; these principles were later developed through studies of biological productivity and ecosystem energetics. In identifying these principles, Forbes showed how ecosystem thinking might proceed directly to the analysis of whole systems without becoming trapped in the infinitely rich detail of the small components that make up the system.

Forbes's use of a lake to illustrate the concept of the superorganismic unit was very effective because lakes have easily identifiable boundaries, clear points of input and output, and some obvious kinds of internal organization. Forbes's focus on lakes is ironic, given that he was, at the time he wrote his essay, Director of the River Laboratory of the Illinois Natural History Survey and was heavily engaged in directing and collecting information on the Illinois River and its floodplain. Apparently Forbes realized that he could not argue very persuasively for ecosystem thinking if he were to use a river and its floodplain as his example rather than a lake.

The term "ecosystem" is seldom applied to rivers. Persons familiar with the ecosystem concept apparently have a sense of incompatibility in attempting to apply it to a river. Given the essential ingredients of the ecosystem concept as presented by Forbes, it is easy to see why a river cannot easily be an ecosystem. The functionally integrated superorganismic unit described by Forbes and incorporated into our modern ecosystem concept is produced mainly by two sets of phenomena: (1) internal circularity of nutrient mass flux regulated by interconnected chains of biological processes, (2) processing of organic matter by organisms that are physically intermixed and that regulate each others' abundance. Thus mass flux is at the root of the eco-

system concept, and specifically critical are the mass fluxes of organic carbon and of one or two regulatory elements (typically N and P). Flux of organic carbon can be treated as energetics, but a mass flux approach is no more difficult and has the advantage of unifying the treatment of nutrients and carbon.

Defining an Ecosystem by Use of Mass Fluxes

A case can be made that an ecosystem is defined by its internal fluxes in relation to fluxes to it and from it, which can be called boundary fluxes. Fluxes can be defined in various ways, but for present purposes it will be assumed that the internal flux of an element is equal to the rate of passage of the element, per unit area, through biomass; a boundary flux is the rate of passage of an element, per unit area, across the boundary of any spatial subdivision of the biosphere. The focus here is on P, N, and C; fixation of N or C is not treated as a boundary flux because the metabolic action occurs inside the system. Because integration of processes is critical to the ecosystem concept, it is also necessary to restrict spatially the calculation of internal fluxes: internal fluxes must represent processes that are occurring together in an integrated fashion.

Any spatial subdivision of the biosphere will show some amount of boundary flux for nutrients and for organic carbon. A given spatial subdivision will show the characteristics of an ecosystem if boundary fluxes are low in relation to internal fluxes. If the ratio of boundary fluxes to internal fluxes is high, the spatial unit lacks the physical integrity to be called an ecosystem according to the concept of Forbes.

Given that the fluxes of carbon and of nutrients, particularly nitrogen and phosphorus, provide by far the most useful general metrics that we have for comparing ecosystems or making general assessments of ecosystems with respect to various theoretical principles, one primary goal of ecosystem analysis should be the estimation or measurement of these fluxes. At a minimum, an ecosystem should be characterized by its incoming and outgoing boundary fluxes, and by its overall internal fluxes for carbon, nitrogen, and phosphorus. At a finer level of detail, these fluxes should be broken down into components that are identified with specific processes.

Some Simplifying Principles for Mass Flux Analysis

An understanding of mass flux for ecosystems must be achieved through measurements extending over periods of at least one year and preferably several years. Experience shows that an understanding of fluxes for ecosystems is achieved only by degrees: most studies do not produce comprehensive empirical estimates of both internal and boundary fluxes. Even though empirical estimates of fluxes are seldom complete, many kinds of conclusions can be reached without a complete data set, or the range of possibilities can be narrowed substantially by analysis of a data set for which some fluxes have not been measured. Three general principles are especially useful in the calculation and comparison of boundary fluxes and internal fluxes for organic carbon, nitrogen, and phosphorus, and will be used here for analysis of Orinoco River ecosystems.

Estimation of total organic carbon flux resulting from net primary production. For present purposes, internal organic carbon flux is defined as the rate of production of organic matter per unit area. Primary production is one component of this internal flux. If it is not measured directly, it can be estimated from vegetation type and moisture in terrestrial systems (e.g., Lieth and Whitaker 1975) or from standing stock of primary producers in aquatic systems (e.g., Brylinsky and Mann 1973). Because production of heterotrophs is seldom measured directly, an important question is whether or not a reasonable estimate can be made of total internal organic carbon flux if primary production is known. First, an allowance must be made for the internal storage and export of organic carbon. Storage must be measured empirically or reconstructed from historical accumulation rates as shown by net forest biomass accretion or net accumulation of carbon inventory in sediment or soil. In some ecosystems, the accumulation of carbon is either negligible or so low that it can be ignored. A portion of primary production that is not stored is exported, i.e., it is a boundary flux, and usually can be measured empirically. The remainder of primary production is converted to inorganic carbon by heterotrophic respiration, but this occurs through a series of steps during which there is additional production, that contributes to internal flux (Figure 1). If the ratio of growth to assimilation is

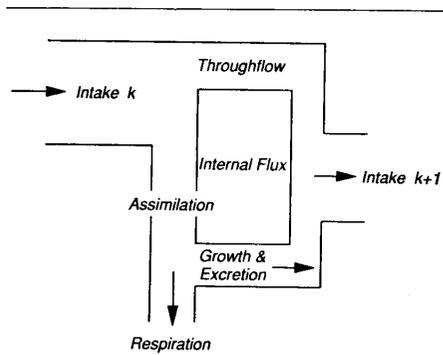


Figure 1. Carbon flux through a heterotrophic compartment showing the basis for calculating internal flux.

known for heterotrophic organisms, the total internal flux ($f_{i,C}$) of organic carbon associated with a particular amount of net primary production (PN), corrected for ecosystem storage (PN'), can be calculated as a series:

$$f_{i,C} = \sum_{k=0}^{\infty} h^k PN' \quad (1)$$

The value of h , which is the ratio of growth to assimilation, varies among different kinds of organisms (excretion also contributes but can usually be ignored). For growing organisms, the values of h appear to fall into three clusters (Peters 1983): (1) homeotherms, for which the ratio is 2-3%, (2) poikilotherms, for which the ratio is approximately 30%, and (3) unicellular organisms, for which the ratio is as high as 80%. Ideally, the value of h would be set specifically for each group of organisms in a given ecosystem. For most ecosystems, it is reasonable to assume that a small portion of organic carbon will flow through the homeotherm compartment, and that the overall value of h will therefore be intermediate between that of small poikilotherms and unicellular organisms. For present purposes, it will be assumed that $h = 0.5$; general conclusions are robust to errors in the estimation of h within a fairly wide range, although more detailed conclusions would require more careful documentation of h .

Internal flux of organic carbon associated with allochthonous sources of organic carbon. Organic carbon crossing a boundary may be processed inside the boundary. The incoming organic carbon is commingled with carbon produced *in situ*, and the outflow of organic carbon is a mixture of the two. However, the net effect of inflowing fixed carbon on internal fluxes can be estimated as the de-

ficit between the incoming and outflowing organic carbon, after correction for storage of organic carbon. The treatment of internal carbon flux generated by incoming allochthonous carbon (IN') can then be identical to the treatment of internal flux generated by primary production, except that the first step (primary production) is omitted from the series because it occurs outside. Thus the equation assumes an extra term as follows:

$$f_{i,C} = \sum_{k=0}^{\infty} h^k PN' + \sum_{k=1}^{\infty} h^k IN' \quad (2)$$

Internal fluxes of nitrogen and phosphorus in relation to organic carbon flux. Internal fluxes of (fixed) nitrogen and phosphorus are defined here in the same way as internal fluxes of organic carbon, i.e., the flux of nitrogen or of phosphorus is defined as the incorporation of these elements into biomass. Because these fluxes are seldom measured directly, it will often be necessary to estimate them from the flux of organic carbon. For organisms that consist primarily of protoplasm and that lack large amounts of organic structural material, a reasonable approximation of the flux of nitrogen and phosphorus in relation to organic carbon can be obtained from the Redfield ratio, which specifies the molar proportions 106:16:1 for phosphorus, nitrogen, and carbon in protoplasm (Redfield 1958). Use of a single ratio overlooks the possibility of luxury consumption, as well as some relatively small variations in the recipe for protoplasm among organisms, but these are usually tolerable errors for purposes of making general estimates.

The Redfield ratio can be used for microbes, algae, and most eukaryotic heterotrophs. However, it cannot be used for higher plants because of the large amount of structural material that is characteristic of these plants. Such structural material is enriched in carbon with respect to nitrogen and phosphorus, and this must be taken into account in making conversions from the processing of organic carbon to the processing of nitrogen and phosphorus. Fortunately, numerous estimates have been made of the ratios of nitrogen and phosphorus to carbon in vascular plants (e.g., Likens *et al.*, 1981; 2040:17:1). Although the fluxes of nitrogen and phosphorus associated with the primary production by higher plants must be estimated according to the lower proportions of nitrogen and phosphorus in higher plants, production at higher trophic levels or by mi-

crobes generated by primary production of vascular plants corresponds to higher relative fluxes of nitrogen and phosphorus because these organisms incorporate additional nitrogen and phosphorus as necessary to synthesize protoplasm from organic carbon in vascular plants. Thus

$$f_{i,P} = \sum_{k=0}^{\infty} (r_{k,P}) PN' + \sum_{k=1}^{\infty} (r_{k,P}) IN' \quad (3)$$

$$f_{i,N} = \sum_{k=0}^{\infty} (r_{k,N}) PN' + \sum_{k=1}^{\infty} (r_{k,N}) IN' \quad (4)$$

Where $r_{k,P}$ is the ratio of P to C in biomass at step k and $r_{k,N}$ is the same for N. For present purposes the Redfield ratios will be used in setting r except for vascular plants, which will be set to the ratio 2040:17:1.

Perspectives on Internal Flux and Boundary Fluxes

Lakes provide useful perspectives on the relative sizes of the internal and boundary fluxes for ecosystems. The range of fluxes for lakes can be estimated through the use of a simple model based on the foregoing principles used in conjunction with a range of characteristics that encompass most lakes. For organic carbon, the assumptions are as follows: (1) organic carbon in the inflowing water between 5 and 15 mg/l, (2) a hydraulic residence time between 0.5 years and five years, (3) a productivity between 50 and 500 g C/m²/yr, and (4) a mean depth between 5 and 50 m. For phosphorus, the assumption for inflow concentrations is 10 or 100 µg/l; for fixed nitrogen, the inflow concentrations are assumed to be either 100 or 1000 µg/l.

Figure 2 shows the placement of lake conditions on a diagram that relates boundary flux to internal flux. For organic carbon, phosphorus, and nitrogen, the median ratio of internal fluxes to boundary fluxes is well above 1, conforming to the expectation that lakes typically show a high degree of internal organization under biological control. For the most extreme cases of high water replacement rates and low production, the ratio of internal to boundary fluxes approaches or goes slightly below 1.0.

The Orinoco River is also shown in Figure 2; its fluxes are estimated from field studies of the Orinoco River between 1982 and 1985, as summarized in Table I. The internal fluxes are based on the metabolic action among the organisms in the river itself; the requirement of reciprocal mass flux connections

TABLE I

CHARACTERISTICS OF THE ORINOCO RIVER MAIN STEM USED IN ESTIMATING THE RATIO OF BOUNDARY FLUXES TO INTERNAL FLUXES FOR ORGANIC CARBON, PHOSPHORUS, AND NITROGEN (DATA FROM LEWIS AND SAUNDERS 1989). DATA FOR CONCENTRATIONS ARE DISCHARGE-WEIGHTED MEANS; MEAN TRANSIT TIME FOR SUSPENDED ORGANISMS AND DISSOLVED SUBSTANCES IS HALF THE MEAN TOTAL TRANSIT TIME FROM HEADWATERS TO MOUTH (ca. 2 WEEKS)

Variable name	Mean value
Mean transit time (weeks)	1
Carbon	
Dissolved organic carbon (mg/l)	4.4
Particulate organic carbon (mg/l)	1.4
Total organic carbon (mg/l)	5.8
Net autotrophic carbon fixation	0.6
Microbial carbon fixation (g/m ² /yr)	220
Internal flux (g/m ² /yr)	450
Boundary flux (g/m ² /yr)	3,120
Flux ratio	0.14
Phosphorus	
Soluble inorganic phosphorus (μg/l)	10
Soluble organic phosphorus (μg/l)	10
Particulate phosphorus (μg/l)	44
Total phosphorus (μg/l)	64
Internal flux (g/m ² /yr)	10
Boundary flux (g/m ² /yr)	34
Flux ratio	0.31
Nitrogen	
Soluble inorganic nitrogen (μg/l)	115
Soluble organic nitrogen (μg/l)	160
Particulate nitrogen (μg/l)	185
Total nitrogen (μg/l)	460
Internal flux (g/m ² /yr)	31
Boundary flux (g/m ² /yr)	260
Flux ratio	0.12

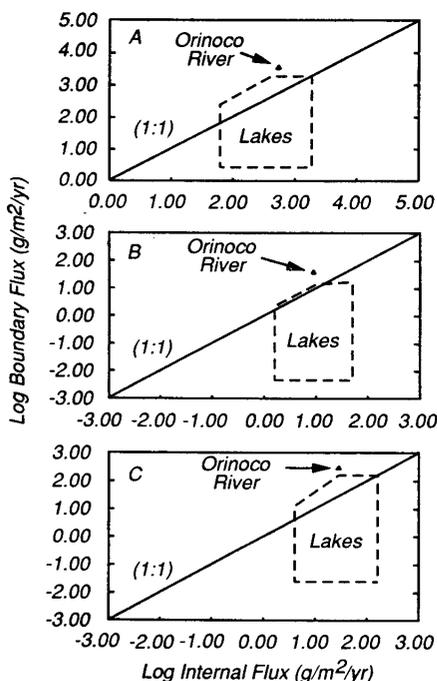


Figure 2. Flux diagrams for C, P, and N showing placement of most lakes and of the Orinoco River.

(recycling) dictates that we cannot average a river with its watershed because the mass flux is not reciprocal. The same is true of the floodplain and the river, which are only partially reciprocal in mass flux.

Figure 2 demonstrates why it is difficult to apply the concept of the ecosystem to the Orinoco River: the boundary fluxes exceed the internal fluxes by an order of magnitude. The river is dominated by transport to such an extent that it does not develop the strong internal regulatory networks that are characteristic of ecosystems.

Organizational Units Larger than Ecosystems: Ecosystem Complexes

If it is not useful or possible to treat the Orinoco River as an ecosystem, then how should it be treated? This is a specific example of an important general problem in ecology, i.e., there is at least one important step in the organizational framework of nature between the ecosystem and the biosphere. This level of organization is plainly visible in the form of functionally coupled segments of landscape that are too large, and too diverse to be single ecosystems, and yet in some respects they are functional units. These regional units, which

are often defined by rivers, can be called ecosystem complexes. The Orinoco River is part of an ecosystem complex, and should be studied in this context, rather than as an ecosystem.

The necessity for thinking in terms of mass flux for organic carbon and critical nutrients is no less applicable to an ecosystem complex than to an ecosystem itself. In fact, it may be even more essential that an ecosystem complex be analyzed in this manner because the internal parts of an ecosystem complex are so diverse physically and

biologically that it is almost impossible to analyse the entire complex meaningfully without thinking in terms of mass flux.

While ecosystems can be defined by circularity of mass flux, the ecosystem complex can be defined by continuity of mass flux. Within the watershed boundary of the Orinoco River, there is strong linear continuity of mass flux. For example, phosphorus released by weathering from rocks in upstream segments of the Guayana Shield or the Andes may find its way into soils and vegetation of terrestrial ecosystems

and subsequently be released into flowing waters that enter the Orinoco River.

It is necessary to distinguish two kinds of functional components in an ecosystem complex: (1) those for which the boundary fluxes are small in relation to the internal fluxes, and (2) those for which the boundary fluxes are large in relation to the internal fluxes; a 1:1 ratio of fluxes is a reasonable dividing line between these two types. Components of the first category are ecosystems; components of the second category are transport pathways that connect ecosystems (Figure 3).

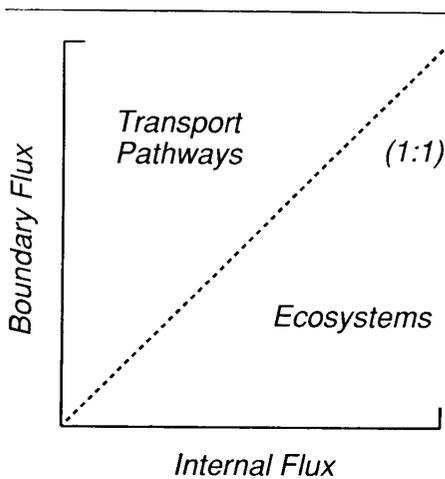


Figure 3. Basis for separating ecosystems from transport pathways.

The gross structure of an ecosystem complex is defined by the spatial configuration of ecosystem clusters and transport pathways. The Orinoco River ecosystem complex has five parts; two of these are ecosystem clusters and the other three are transport pathways (Figure 4). One of the ecosystem clusters consists of a diverse assemblage of terrestrial ecosystems, including dry forest, moist forest, savanna, and montane environments. The second cluster, which is

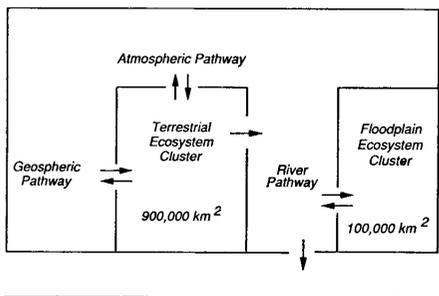


Figure 4. Orinoco ecosystem complex components.

almost as diverse, consists of floodplain, including fringing floodplain along the main channel, internal deltaic floodplain at the mouth of the Apure, and coastal deltaic floodplain near the mouth of the Orinoco. Although all rivers with floodplains have terrestrial and floodplain ecosystem clusters, subdivision of the clusters varies widely from one river to the next (Hamilton and Lewis, 1990a).

The remaining three components of the Orinoco complex are transport pathways. The river itself is a transport pathway because of its high ratio of boundary flux to internal flux. In addition, the atmosphere is a significant transport pathway, as is the geosphere.

The terrestrial component of the Orinoco ecosystem complex reflects watershed diversity in moisture, elevation, slope, and geology. Ideally, we should be able to portray for the full spectrum of ecosystem types the boundary fluxes and internal fluxes for carbon, nitrogen, phosphorus, and possibly other elements. However, our state of knowledge is not sufficiently advanced to allow this. We know most of the fluxes for some of the parts and some of the fluxes for most of the parts, but we do not know all of the fluxes for all of the parts, nor do we have any immediate prospect of knowing them all. Flux information that is presently available falls mostly into two main categories: (1) outgoing boundary flux estimated from mass balance measurements for the Orinoco and its tributaries, and (2) more detailed flux information for the Caura River and the Apure River basins.

A summary of fluxes for the Caura River basin is shown in Figures 5 and 6. The boundary fluxes are based on measurements of atmospheric deposition, mass transport of the Caura River, and weathering rates of shield rock as calculated from the ratios of elements in atmospheric deposition and in the flow of the Caura River as reported by Lewis (1986) and Lewis *et al.* (1986, 1987). The internal fluxes of the Caura basin have not been studied directly. However, information from the studies at San Carlos de Rio Negro under generally similar conditions at the southern edge of the Orinoco drainage can be used for present purposes. Information for the San Carlos site is taken primarily from the summary of Jordan (1985).

For organic carbon, nitrogen, and phosphorus, the ratio of boundary fluxes to internal fluxes is extremely low in the Caura forest (Figure 6), indicating the high degree of internal

integration that is characteristic of tropical moist forest. The ratio of internal to external fluxes exceeds the ratio that is characteristic of most lakes, despite the fact that large amounts of water move through the watershed. In fact it is possible to make a comparison of the Caura River forest ecosystem with an aquatic ecosystem on the same site; the calculation is not entirely hypothetical because of the existence of the Guri Reservoir in the adjoining Caroni watershed. The ratio of internal to external fluxes is about an order of magnitude higher for the tropical moist forest than for a reservoir on the same site. This is explained primarily by differences in primary production. Whereas the tropical moist forest generates as much as 1000 g C/m²/yr, impounded waters on the same site would be extremely oligotrophic because of low nutrient concentrations, and would generate about 25 g C/m²/yr (Guri Reservoir: Lewis and Weibezahn 1976). This illustrates the great potential of tropical moist forest to sustain high productivity in environments that are very poor in nutrients.

The boundary fluxes for phosphorus in the Caura forest are striking in several ways. First, the atmospheric source of phosphorus is very substantial by comparison with either the geospheric source or the total runoff losses of phosphorus. A portion of this phosphorus may actually recycle within the basin. However, it appears from the chloride concentrations and from the significant particulate component of phosphorus deposition that the bulk of phosphorus entering from the atmosphere originates outside the watershed, and probably from the north where phosphorus is more readily brought into the atmosphere from dry soil surfaces. Thus there may be a continual long-distance phosphorus enrichment of the Caura River forest through the atmosphere. Also notable is the geospheric source of phosphorus for the Caura River watershed. The parent material of the Caura River watershed is among the most resistant to weathering that can be found. In addition, the phosphorus content of the shield material is low (approximately 0.1% by mass). However, the very high amount of precipitation and continually warm temperatures produce surprisingly high weathering rates (1.8 cm per thousand years), which in turn lead to the liberation of significant amounts of phosphorus from the geospheric source. Some of this phosphorus may not be available to plants because it is produced below the root

zone. However, if it were all available, it could sustain a net primary production of 40 g C/m²/yr, independently of any recycled phosphorus. This is approximately 4% of the expected net production of the forest. Thus at least from the viewpoint of phosphorus, the regeneration of lost biomass could occur rather quickly (25 years for complete regeneration), even if regeneration were not sustained by recycling mechanisms. An interesting point for future study is the degree of separation between the biological uptake zone and the production of available forms of phosphorus through weathering.

The Caura River watershed also shows a sizeable net retention of phosphorus (about 30%). Although it is typical to think of the geosphere as being exclusively a source of phosphorus, the geosphere is a significant sink for phosphorus in the Caura River basin. Several mechanisms may explain this, the most likely of which is probably the formation of iron and aluminum phosphates below the root zone, leading to the immobilization of phosphorus.

Although the very high ratio of internal flux to boundary flux for phosphorus has already been noted, one obtains a somewhat different perspective from the concentrations of phosphorus in water flowing from the drainage. The discharge-weighted phosphorus concentration in the Caura River is 20 µg/l, of which about 50% is soluble. The uptake capabilities of vascular plant roots and their associated microorganisms are fully functional down to the range of 1 µg/l of soluble phosphorus. The concentrations of phosphorus in the Caura River from this perspective are surprisingly high. Furthermore, the concentrations of phosphorus are not any lower in the Caura River than they are in rivers supporting ecosystems that are less productive (Table II). In other words, the retention capabilities of the tropical moist forest in the Caura River are impressive in relation to the internal uses of phosphorus, but are not substantially higher than the retention capabilities of some other kinds of terrestrial ecosystems.

Nitrogen presents a very different picture, as might be expected in view of the absence of nitrogen from rock and the numerous mechanisms for transport of gaseous nitrogen across ecosystem boundaries. The concentrations of fixed nitrogen in atmospheric deposition are fairly high in absolute terms, but this is not surprising because of the universal presence of fixed nitrogen in precipitation. Despite the high absolute flux

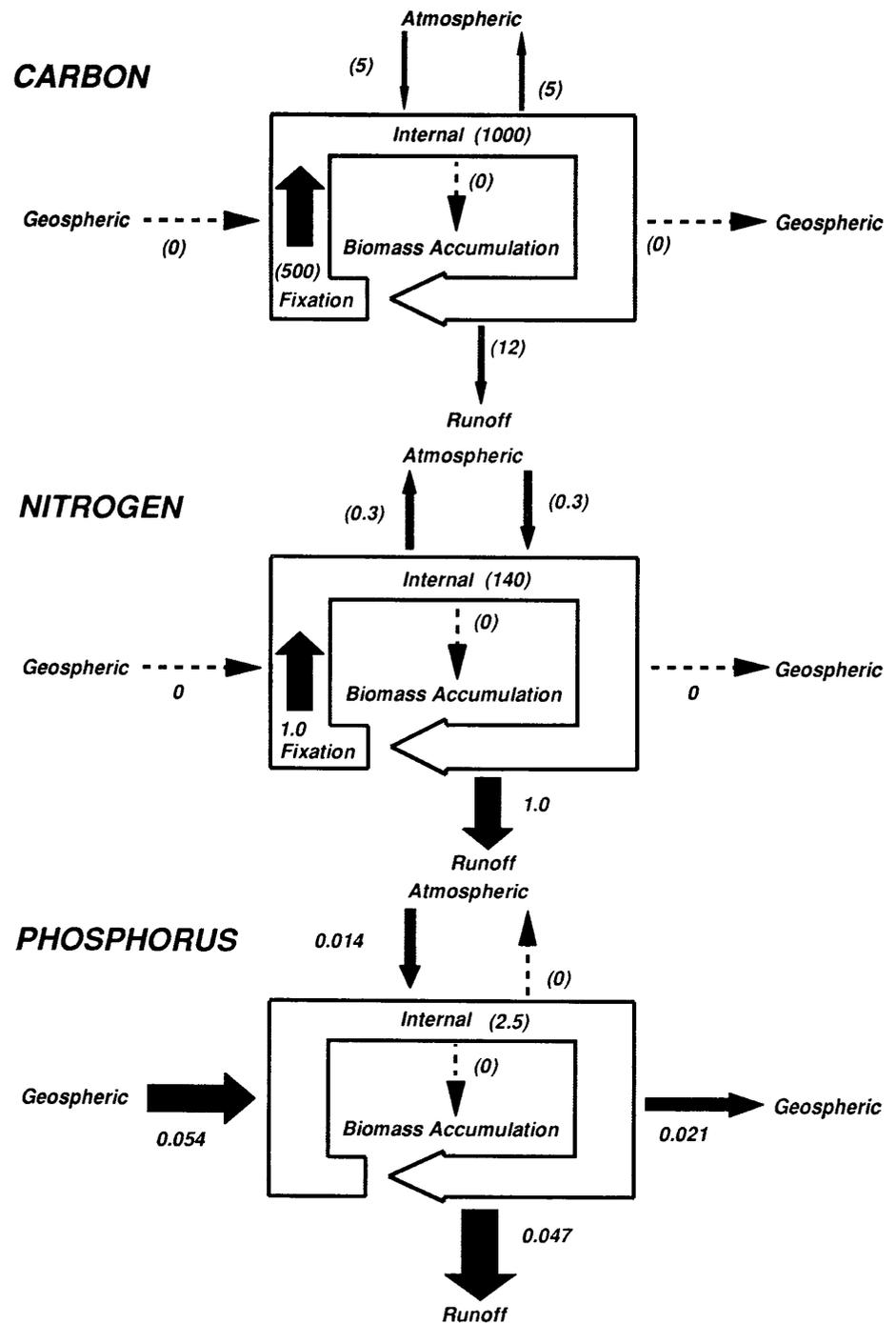


Figure 5. Fluxes of C, N, and P for Caura forest ecosystems.

of fixed nitrogen through the atmosphere, the boundary flux of fixed nitrogen is actually smaller in relation to the internal flux of nitrogen than is the total or even the atmospheric boundary flux for phosphorus. Thus, despite the higher absolute magnitude of the nitrogen flux, the system would, in the absence of nitrogen fixation, quickly enter a severe nitrogen deficit.

Also significant for nitrogen is the outgoing boundary flux for fixed nitrogen, which exceeds the incoming boundary flux for fixed nitrogen by several fold. By comparison, the outgoing boundary flux for phosphorus is actually less than the incoming boundary flux. The high losses are well illustrated by the discharge-weighted concentrations for fixed nitrogen in the Caura River watershed. The concentration of total N for

**Internal vs. Boundary Fluxes
Caura Forest**

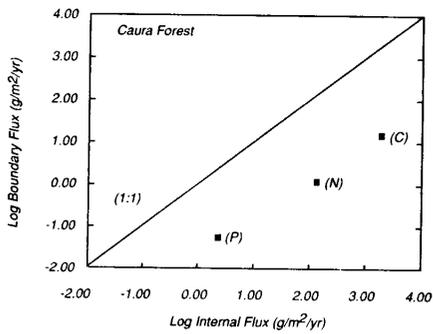


Figure 6. Flux diagram for Caura forest ecosystems.

the Caura River on a discharge-weighted basis is 400 $\mu\text{g/l}$, of which 60 $\mu\text{g/l}$ is nitrate and 40 $\mu\text{g/l}$ is ammonium. These are extraordinary losses, given the supposed efficiency of tropical moist forests in retaining nutrients. As in the case of phosphorus, the rates of loss for fixed nitrogen are at least as great for the Caura River system as they are for much less productive systems, and the outgoing

concentrations of fixed inorganic nitrogen far exceed the uptake thresholds for microorganisms and roots.

The imbalance between the incoming and outgoing boundary flux for fixed nitrogen is made up by nitrogen fixation. Although rates of denitrification have not been measured in the Caura River watershed, measurements at other sites indicate the rates of denitrification are considerably smaller than nitrogen fixation rates. The nitrogen fixation rate for the Caura River drainage is at least 1 $\text{g/m}^2/\text{yr}$; it exceeds this by the rate of denitrification loss, which would be near 0.3 $\text{g/m}^2/\text{yr}$ if it resembles that of similar Amazon sites that have been studied (Jordan *et al.*, 1982).

For organic carbon, the incoming boundary flux is lower in proportion to internal fluxes than for nitrogen and phosphorus. Given that a significant outgoing boundary flux associated with release of volatile organics is likely but undocumented, net gain of fixed organic carbon from the atmosphere may be negligible. The outgoing boundary flux for organic carbon in runoff is high, but is not of much functional significance because organic carbon, in contrast to N

and P, is not significant as a limiting nutrient. It is clear from the carbon yields and from the concentrations of carbon in the Caura River that the Caura River forests are not particularly efficient in retaining carbon; the concentrations and yields overlap broadly with those of other kinds of terrestrial ecosystems. The outgoing boundary flux for organic carbon in the Caura River basin is among the highest known for mature forests, primarily because the concentration of dissolved organic carbon originating from mature forests has a tendency to be homeostatic in relation to runoff (Schlesinger and Melack 1981). For this reason, forests that have a very high throughput of water, as does the Caura River basin, have very high yields of organic carbon. However, the total boundary flux of carbon is not very high in relation to the internal organic carbon flux.

Information on fluxes is much sketchier for terrestrial ecosystems other than those of the Caura River, although mass balance has been studied for the Apure River drainage in some detail. (Saunders and Lewis 1988, 1989a). The outgoing boundary fluxes for carbon, nitrogen, and phosphorus have

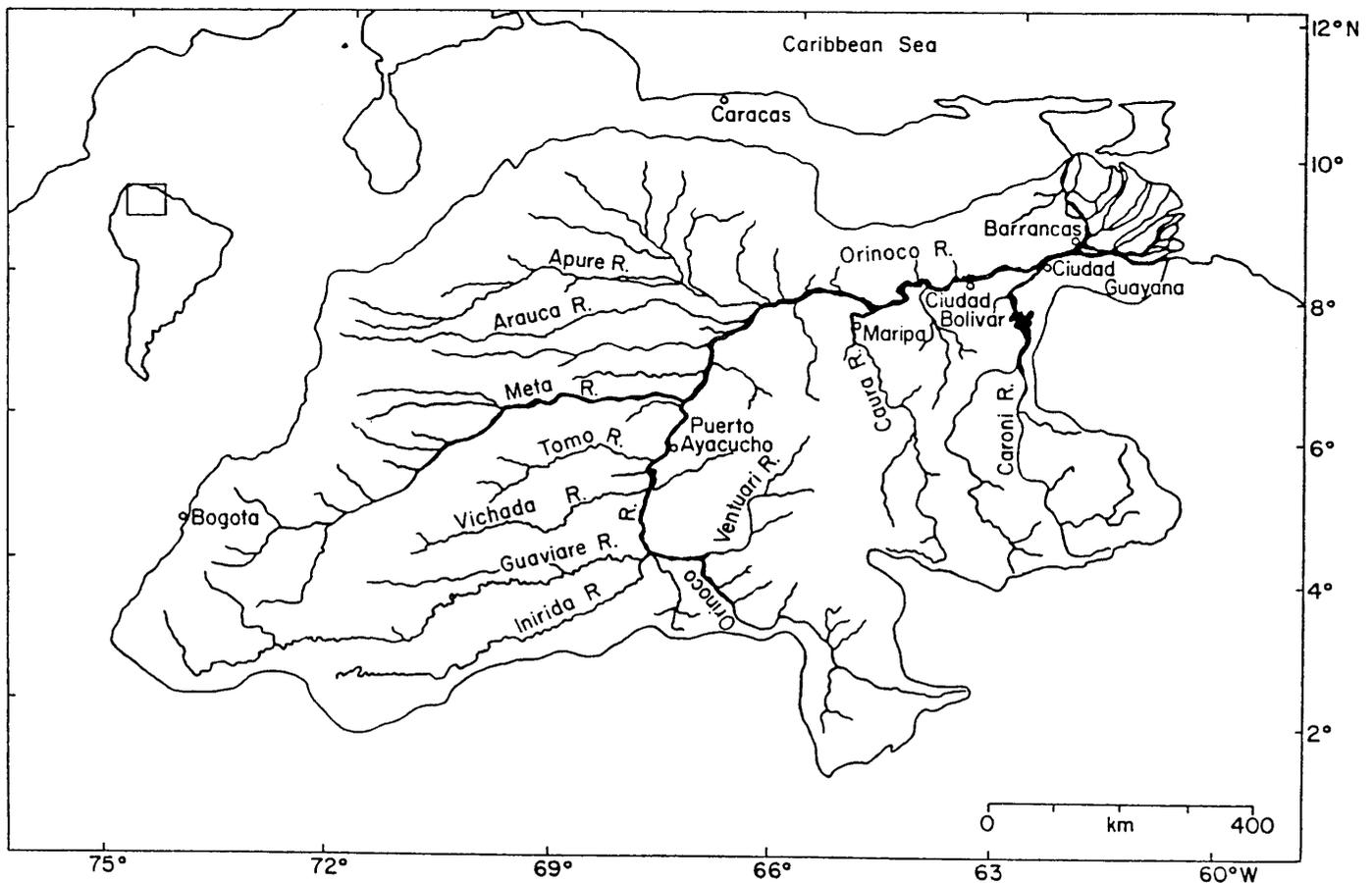


Figure 7. The Orinoco River drainage.

been documented for all of the major tributaries to the Orinoco (Figure 8) and they provide a useful indication of the degree of diversity among terrestrial ecosystems with respect to boundary flux. The results are summarized in Table III. The watersheds fall easily into three groups, on the basis of phosphorus and to some extent inorganic nitrogen: (1) watersheds draining the Guayana Shield, (2) watersheds draining alluvial plain, and (3) watersheds draining alluvial plain with headwaters in the Andes. The highest boundary fluxes of phosphorus are for watersheds with headwaters in the Andes; there is a strong inverse relation of concentration with runoff in this group. Watersheds on alluvial plain lacking contact with the Andes have extraordinarily low boundary fluxes for both nitrogen and phosphorus. Terrestrial ecosystems in these areas clearly warrant further study from the viewpoint of mass flux because of their high efficiency in conserving nitrogen and phosphorus. The forests of the Guayana Shield are similar to each other (the Caroni shows lower P probably because of sedimentation in the Guri Reservoir), particularly with regard to phosphorus, and are not notably more efficient in retaining nutrients than the savanna areas.

The Orinoco Floodplain Ecosystem Cluster

The floodplain component of the Orinoco complex also consists of a diverse cluster of ecosystems. These fall into three groups: (1) the fringing floodplain of the main stem, (2) the internal delta floodplain, primarily of the llanos, and (3) floodplain of the coastal delta (Hamilton and Lewis 1990). The boundary fluxes for the delta and llanos components are still unknown, but the fluxes of carbon, nitrogen, phosphorus, and other elements through the fringing floodplain have been estimated through mass balance studies over long segments of the Orinoco River. Measurements of change in mass transport between an upstream point and a downstream point, combined with knowledge of metabolic fluxes during transport, lead to estimates of the net effect of the floodplain. In addition, small segments of floodplain have been studied intensively, especially in the vicinity of Lake Tineo near Ciudad Bolívar (Hamilton and Lewis 1987).

The net flux of organic carbon, nitrogen, and phosphorus from the fringing floodplain of the Orinoco

TABLE II

COMPARISON OF CONCENTRATIONS ORIGINATING FROM THE CAURA RIVER AND FROM SOME UNDISTURBED ECOSYSTEMS HAVING LOW NUTRIENT OUTPUTS (SOURCES: LEWIS 1986, LIKENS *et al.*, 1977, LEWIS *et al.*, 1984, SCHINDLER *et al.*, 1976)

	Runoff (mm/y)	Total P $\mu\text{g/l}$	Total N
Caura Forest	2,400	20	400
Hubbard Brook, N. H.	830	2	480
Summit County, Colorado	420	8	200
Canadian Shield, Ontario	277	18	340

River is very close to zero (Hamilton and Lewis 1987, Figure 9). For phosphorus, is not a surprising result, in that phosphorus balance of the floodplain is likely to reflect the approach to long-term mass equilibrium of the floodplain for total soluble and suspended materials. The zero net flux of carbon and nitrogen for the floodplain is more significant. The floodplain supports a large amount of primary production by phytoplankton, macrophytes, and flooded forest (Hamilton and Lewis 1987). A large amount of nitrogen fixation occurs on the floodplain, especially during the period of low water. High primary production and high nitrogen fixation would be expected to enrich the floodplain in organic carbon and fixed nitrogen. This enrichment then should be reflected in higher concentrations of organic carbon and fixed nitro-

gen during periods of floodplain flushing. However, this is not the case. Organic carbon and fixed nitrogen are metabolized efficiently within the floodplain. The annual cycle of events on the floodplain is more accurately portrayed as synthesis and degradation within the floodplain, rather than synthesis and export from the floodplain. The same is true of plankton production: the export of plankton from the floodplain to the river is extremely small, contrary to expectation (Lewis 1988, Saunders and Lewis 1989b). With respect to organic carbon, fixed nitrogen, and suspended organisms, the Orinoco River floodplain functions primarily as if it were a closed system rather than an open system.

Studies within the floodplain indicate that the peculiar and unexpected ability of the Orinoco floodplain

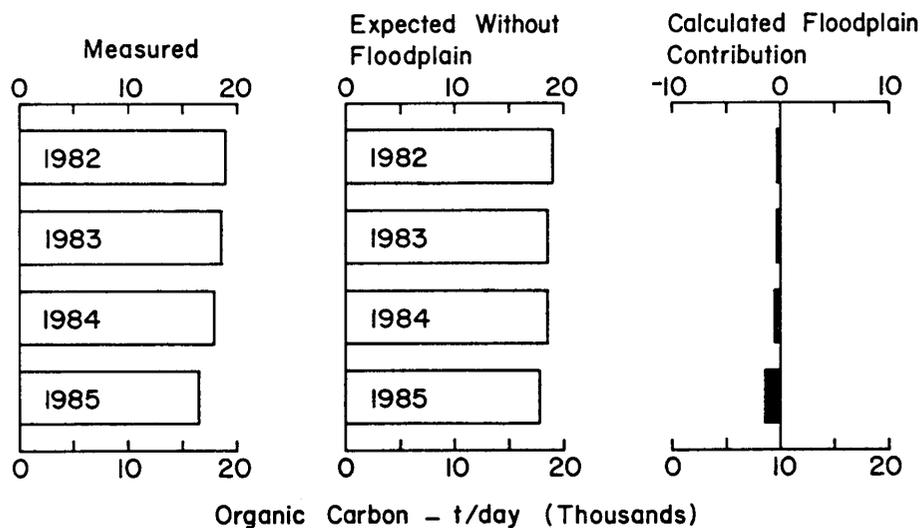


Figure 8. Net carbon flux through the Orinoco fringing floodplain as calculated by mass balance along the main stem.

TABLE III

CONCENTRATION ($\mu\text{g}/\text{l}$ FOR N, P, mg/l FOR C) AND BOUNDARY FLUXES
FOR MAJOR TRIBUTARIES OF THE ORINOCO RIVER. SOURCES:
LEWIS AND SAUNDERS 1990, WEIBEZAHN 1985

River	Runoff, mm/yr	P	$\mu\text{g}/\text{l}$			$\text{g}/\text{m}^2/\text{yr}$			
			N *	C	P	N *	C		
Shield Rivers									
Upper Orinoco	950	17	—	(95)	6.6	.016	—	(.091)	6.3
Ventuari	1,570	17	—	(81)	4.8	.026	—	(.127)	7.5
Caura	2,400	20	400	(100)	5.5	.046	0.960	(.240)	13.2
Caroni	1,632	11	300	(122)	5.8	.018	0.490	(.199)	9.5
Plains Rivers									
Atabapo	2,000	4	—	(32)	10.5	.007	—	(.064)	21.0
Vichada	646	14	—	(23)	4.3	.009	—	(.015)	2.8
Plains Rivers with Montane Headwaters									
Guaviare	1,850	48	—	(79)	8.5	.088	—	(.146)	15.6
Meta	1,600	86	—	(120)	13.3	.138	—	(.192)	21.2
Apure	361	188	960	(178)	9.8	.068	0.347	(.064)	3.5

* Total N if available; inorganic N shown in parentheses.

to conserve organic carbon and fixed nitrogen is accounted for to a large extent by physical characteristics of the floodplain. The flowing waters of the Orinoco are separated from the floodplain by a natural levee. Water flows into the floodplain at discrete points corresponding to breaks in the levee. After entering the floodplain the water flows for long distances parallel to the levee before regaining contact with the river. Along the pathway of flow, the water passes through sequences of depressions that correspond to the floodplain lakes visible during the dry season (Hamilton and Lewis 1990a). Each of these floodplain lakes and the

surrounding floodplain forest is really a separate ecosystem. The lakes diverge in their physical, chemical, and biological characteristics as the water recedes (Figure 10). Thus the fringing floodplain of the Orinoco consists of a large cluster of individual floodplain ecosystems that are connected serially along the path of flow.

The serial connection of floodplain ecosystems in the fringing floodplain probably explains the high efficiency of the Orinoco River in processing organic carbon, fixed nitrogen, and suspended organisms. Dissolved and particulate material originating in one ecosystem will pass through several other ecosystems before becoming physically connected to the river. Serially arranged systems of this type can show high efficiency in the processing of organic material because of higher retention time and greater contact with biologically active surfaces for suspended or dissolved material. Macrophyte mats may play a special role in maintaining the high processing efficiency of the floodplain (Hamilton *et al.* 1990). Water flowing from one ecosystem to the next passes through extensive macrophyte beds. These macrophyte beds offer very large amounts of underwater surface area on which processing of organic material can occur. Upstream-downstream comparisons within the floodplain indicate that a

significant amount of the composting function for organic matter in the floodplain occurs at the junction between floodplain ecosystems in series, and specifically through the action of macrophyte mats.

Mass fluxes characteristically show seasonal variation. This is true even for tropical moist forest. However, the degree of seasonal variation in mass flux for the fringing floodplain of the Orinoco River, and for floodplains in general, is extreme (Figure 11). During the dry season, the ratio of internal flux to boundary flux is high. During the season of inundation, the ratio of internal

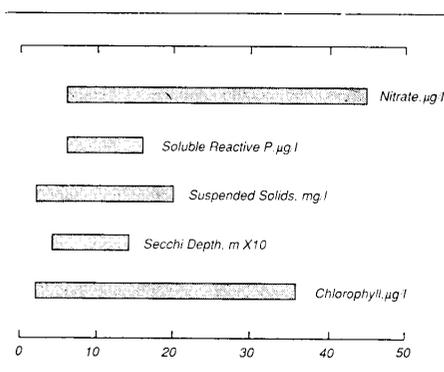


Figure 9. Divergence among floodplain ecosystems of the Orinoco fringing floodplain after inundation (data from Hamilton and Lewis 1990b).

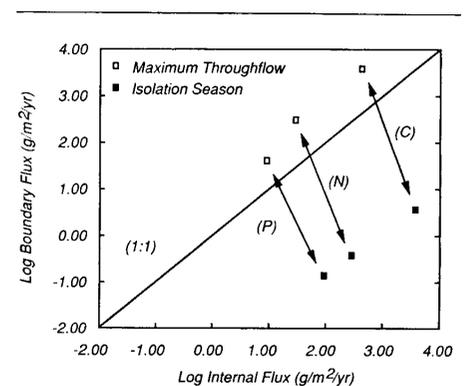


Figure 10. Flux diagram for the fringing floodplain.

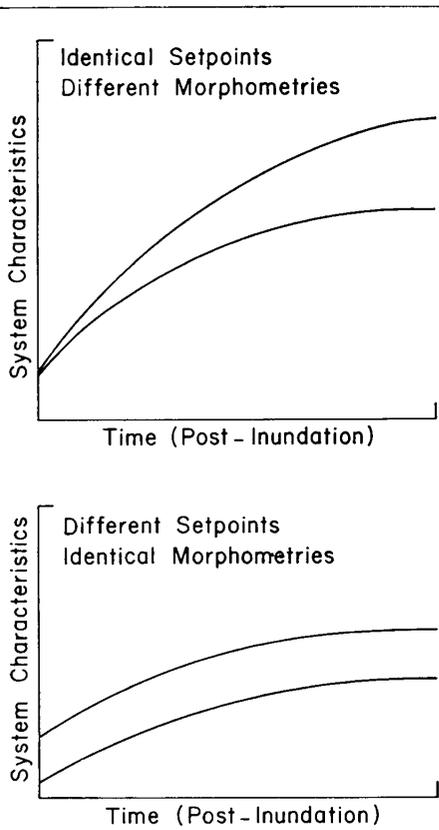


Figure 11. Illustration of the setpoint/divergence principle. System characteristics (productivity, biotic composition, mass balance, etc.) are to a large degree determined by setpoint, which is related to distance along the river, and by basin morphometry, which explains subsequent divergence.

to boundary fluxes crosses the 1:1 ratio that separates ecosystems from transport pathways. Because the long-term mean ratio of internal to boundary fluxes is well below 1:1, there is no difficulty in classifying floodplain environments as ecosystems rather than transport pathways. However, the brief transgression over the 1:1 threshold each year signifies a special kind of mass flux regime. The appropriate designation for this functional regime is disturbance. In fact, a good operational definition of a disturbance in the context of mass flux that has been presented here is any environmental factor that causes the ratio of internal flux to boundary flux for an ecosystem to cross temporarily over the 1:1 ratio that separates transport pathways from ecosystems. Other definitions are possible; Resh *et al.* (1988) would exclude annual flooding from the definition of disturbance because of its predictability.

The disturbance phase each year causes the functional boundaries between adjacent floodplain ecosys-

tems to be temporarily obliterated. The adjacent floodplain basins that are separate during the dry season become essentially uniform and contiguous with respect to nutrient chemistry and biological properties during the season of inundation. However, following inundation, these adjacent systems reestablish their individuality. Although they would appear in many cases to be very similar to each other, they diverge significantly in their chemical, physical, and biological properties after the inundation has ceased. The set of common conditions established by disturbance may be termed a setpoint. For adjacent ecosystems along the Orinoco River fringing floodplain, the setpoint includes the common major ion chemistry, nutrient chemistry, external organic carbon loading, turbidity, temperature, and inventory of suspended organisms as determined by the water entering the floodplain from the main stem of the Orinoco River during inundation. Inundation returns adjacent ecosystems to the setpoint each year, and these ecosystems then evolve along separate trajectories during which their biological, chemical, and physical properties diverge remarkably toward separate end points. The alternating divergence and convergence of ecosystems, although multivariate, can be represented diagrammatically as shown in Figure 12. Specific examples are available for water chemistry (Hamilton and Lewis 1990b), zooplankton (Vasquez 1984, Twombly and Lewis 1987, 1989), and fishes (Rodriguez and Lewis 1990).

The concept of setpoints and divergence from setpoints through successional processes must be supplemented by recognition of the fact that there may be a gradient of setpoints (Table IV). The suspended organism inventory and the water chemistry for the lower portion of the Orinoco mainstem is not necessarily the same as for the upper Orinoco fringing floodplain. In general terms, the variation in ecosystem properties along the fringing floodplain is explained by two sets of factors: (1) the setpoint itself, and (2) physical factors (mostly morphometry) that result in deviation of individual systems from each other by successional processes after the setpoint is established (Figure 11). In fact, ecosystems can be clustered statistically by distance along the river (setpoint) and basin morphometry (Figure 12).

The concept of disturbance, and the subsidiary concepts of setpoint and successional divergence from

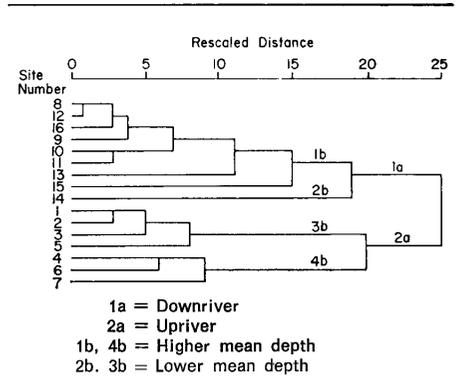


Figure 12. Cluster analysis based on chemical and biological variables measured in 16 lakes on a single sampling date in 1986, showing the influence of setpoint (upriver, downriver) and divergence based on morphometry (mean depth).

setpoint provide a framework within which the widely varying characteristics of the many ecosystems that make up the ecosystem cluster of the Orinoco floodplain can be organized. Although there has been some progress in establishing overall characteristics of the fringing floodplain, coverage should be extended to other parts of the floodplain and the functional diversity of the floodplain should be studied more thoroughly within the framework of natural disturbance and recovery from disturbance.

Ecosystem Complexes and Human Societies

Ecosystem complexes are large units of nature that show continuity of mass flux and that bridge the gap between ecosystem and biosphere. We might hope that a few such units could be preserved entirely for future study. However, ecosystem complexes are so large that it seems unrealistic to hope that any of them will remain entirely unexploited. Even now, ecosystem complexes can be viewed in their natural state only at very high latitudes and very low latitudes. The next best alternative is to study the remaining natural ecosystem complexes, including the Orinoco River basin, intensively while they remain more or less natural. For the future, the exploitation of ecosystem complexes should ideally occur with some view toward preserving characteristic parts of the complex, and taking into account the continuity of mass flux within the complex.

Conclusions

Ecosystem science is presently not well suited to provide a

framework for study of large integrated units of landscape that are too diverse to be classified as ecosystems. There exists a unit of ecological organization between the single ecosystem and the biosphere. This unit of organization may be called the ecosystem complex because it incorporates multiple ecosystems joined by transport pathways. The treatment of large rivers and their watersheds as ecosystem complexes allows the functional unity within a large river system to be recognized without forcing these large and diverse functional units into compliance with the ecosystem concept, with which they are not compatible. The organizational framework provided by the ecosystem complex is well served by an initial emphasis on boundary fluxes and internal fluxes of carbon, nitrogen, and phosphorus for specific components of the complex and for characteristic ecosystem types within the complex. The internal fluxes reflect the degree of internal organization for individual components or ecosystems, and the boundary fluxes show the degree of communication among components.

ACKNOWLEDGMENTS

This work is a contribution a collaborative Venezuelan-U.S. ecological investigation of the Orinoco River and its floodplain (PECOR). Logistical and financial support were provided by the Venezuelan Ministerio del Ambiente y de los Recursos Naturales Renovables and by the U.S. National Science Foundation through grant BSR8604655.

REFERENCES

Brylinsky, M. and K. H. Mann (1973): An analysis of factors governing productivity in lakes and reservoirs. *Limnology and Oceanography* 18: 1-14.

Forbes, S. A. (1887): The lake as a microcosm. *Bulletin of the Science Association of Peoria, Illinois* 1887: 77-87.

Hamilton, S. K. and W. M. Lewis, Jr. (1987): Causes of seasonality in the chemistry of a lake on the Orinoco River floodplain Venezuela. *Limnol. Oceanogr.* 32: 1277-1290.

Hamilton, S. K. and W. M. Lewis, Jr. (1990a): Physical characteristics of the fringing floodplain of the Orinoco River, Venezuela. *Interciencia* 15: ...

Hamilton, S. K. and W. M. Lewis, Jr. (1990b): Basin morphology in relation to chemical and ecological characteristics of lakes on the Orinoco River floodplain, Venezuela. *Arch. Hydrobiol.* (In press).

Hamilton, S. K., S. J. Sippel, W. M. Lewis, Jr., and J. F. Saunders, III (1990): Zooplankton abundance and evidence for its reduction by macrophyte mats in two Orinoco floodplain lakes. *J. Plank. Rsch.* 12: 345-363.

TABLE IV
CONDITIONS DEFINING THE EXTREMES OF INUNDATION SETPOINT
ALONG THE ORINOCO

	Blackwater Extreme	Whitewater Extreme
Major ions (mg/l)		
Ca ⁺⁺	0.6	16.2
Mg ⁺⁺	0.2	3.0
Na ⁺	1.2	2.3
K ⁺	0.6	2.2
HCO ₃ ⁻	4.8	61.8
SO ₄	0.3	10.7
Cl ⁻	0.4	1.7
Nutrients (µg/l)		
NO ₃ -N	70	135
NH ₄ -N	37	43
TSN	279	444
PN	127	512
Total N	406	956
PO ₄ -P	2.6	44
TSP	8.5	60
PP	9.9	128
Total P	18.4	188
Organic carbon (mg/l)		
Particulate	1.0	3.6
Dissolved	4.5	6.2
Suspended load (mg/l)		
Total	13	235
Organisms		
Phytoplankton (µg/l chl a)	0.044	0.355
Zooplankton (indiv/l)	10	60
Bacteria (indiv/ml)	3 x 10 ⁵	5 x 10 ⁵
Jordan, C. F. (ed.) (1985): <i>Amazonian Rain Forests</i> . Springer-Verlag, NY 133 p.	Lewis, W. M. Jr. and J. F. Saunders, III (1989): Concentration and transport of dissolved and suspended substances in the Orinoco River. <i>Biogeochemistry</i> 7: 203-240.	
Jordan, C., W. Caskey, G. Escalante, R. Herrera, F. Montagnini, R. Todd, and C. Uhl (1982): The nitrogen cycle in a "tierra firme" forest on oxisol in the Amazon territory of Venezuela. <i>Plant and Soil</i> 67: 325-332.	Lewis, W. M. Jr. and F. H. Weibezahn (1976): Chemistry, energy flow, and community structure in some Venezuelan fresh waters. <i>Arch. Hydrobiol. Suppl.</i> 50: 145-207.	
Lewis, W. M. Jr. (1986): Nitrogen and phosphorus runoff losses from a nutrient-poor tropical moist forest. <i>Ecology</i> 67: 1275-1282.	Lewis, W. M. Jr., J. F. Saunders, III, D. W. Crumpacker, Sr. and C. Brendecke (1984): <i>Eutrophication and Land Use</i> : Lake Dillon, Colorado. Springer, NY.	
Lewis, W. M. Jr. (1988): Primary production in the flowing waters of the Orinoco in relation to its tributaries and floodplain. <i>Ecology</i> 69: 679-692.	Lewis, W. M. Jr., J. F. Saunders, III, S. N. Levine, and F. H. Weibezahn (1986): Organic carbon in the Caura River, Vene-	

- zuela. *Limnology and Oceanography* 31: 653-656.
- Lewis, W. M. Jr., S. Hamilton, S. Jones, and D. Runnells (1987): Major element chemistry, weathering, and element yields for the Caura River drainage, Venezuela. *Biogeochemistry* 4: 159-181.
- Lewis, W. M. Jr., and J. F. Saunders, III (1990): Chemistry and transport by the Orinoco main stem and lower tributaries. in H. Alvarez, F. H. Weibezahn, and W. M. Lewis, Jr. *The Orinoco River* (in press).
- Lieth, H. and R. H. Whittaker (eds.): *Primary productivity of the Biosphere*. Springer, NY.
- Likens, G. E., F. H. Borman, R. S. Pierce, J. S. Eaton, and N. M. Johnson (1977): *Biogeochemistry of a Forested Ecosystem*. Springer, NY.
- Likens, G. E., F. H. Bormann, and N. M. Johnson (1981): Interactions between major biogeochemical cycles and terrestrial ecosystems. pp. 93-112 in G. E. Likens (ed.) *Some perspectives on the Major Biogeochemical Cycles*. SCOPE Report 17, Wiley, NY.
- McIntosh, R. P. (1985): *The Background of Ecology*. Cambridge, NY.
- Odum, E. P. (1953): *Fundamentals of Ecology*, 1st edition. Saunders, Philadelphia
- Peters, R. H. (1983): *The Ecological Implications of Body Size*. Cambridge, N.Y.
- Redfield, A. C. (1958): The biological control of chemical factors in the environment. *American Scientists* 46: 205-221.
- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace and R. C. Weissmar (1988): The role of disturbance in stream ecology. *J. N. Am. Benthol. Soc.* 7: 433-455.
- Rodríguez, M. A. and W. M. Lewis, Jr. (1989): Diversity and species composition of fish communities of Orinoco Floodplain lakes. *National Geographic Research*. 6: 319-328.
- Saunders, J. F. III and W. M. Lewis, Jr. (1988): Transport of phosphorus, nitrogen, and carbon by the Apure River, Venezuela. *Biogeochemistry* 5: 323-342.
- Saunders, J. F. III and W. M. Lewis, Jr. (1989a): Transport of major solutes and the relationship between concentrations and discharge in the Apure River, Venezuela. *Biogeochemistry* 8: 101-113.
- Saunders, J. F. III and W. M. Lewis, Jr. (1989b): Zooplankton abundance in the lower Orinoco River, Venezuela. *Limnology and Oceanography* 34: 395-407.
- Schindler, D. W., R. W. Newbury, K. G. Beatty, and P. Campbell (1976): Natural water and chemistry budgets for a small pre-Cambrian lake basin in Central Canada. *Journal of the Fisheries Research Board of Canada* 33: 2526-2543.
- Schlesinger, W. H. and J. M. Melack (1981): Transport of organic carbon in world rivers. *Tellus* 33: 172-187.
- Tansley, A. G. (1935): The use and abuse of vegetational concepts and terms. *Ecology* 16: 284-307.
- Twombly, S. and W. M. Lewis, Jr. (1987): Zooplankton abundance and species composition in Laguna la Orsinera, a Venezuelan floodplain lake. *Arch. Hydrobiol. Suppl.* 79: 87-107.
- Twombly, S. and W. M. Lewis, Jr. (1989): Factors regulating cladoceran dynamics in a Venezuelan floodplain lake. *J. Plankton Research* 11: 317-333.
- Vásquez, E. (1984): Estudio de las comunidades de rotíferos del Orinoco Medio, Bajo Caroní y algunas lagunas de inundación. *Mem. Soc. Cienc. Nat. La Salle* 44: 95-108.
- Weibezahn, F. H. (1985): Concentraciones de especies químicas disueltas y transporte de sólidos suspendidos in el alto y medio Orinoco y sus variaciones estacionales. *Ministerio del Ambiente y de los Recursos Naturales Renovables*, Petróleos de Venezuela, S.A. Informe.