Acta Limnol. Brasil.	Vol. III	77-113	1990

ASPECTS OF PRIMARY PRODUCTIVITY IN THE LOWER PARANA AND PARAGUAY RIVERINE SYSTEM

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RESUMO - ASPECTOS DA PRODUTIVIDADE PRIMÁRIA NO SISTEMA FLUVIAL DO BAIXO PARANÁ E DO BAIXO PARAGUAI

O aporte de matéria orgânica no sistema fluvial do Baixo Paraná e Baixo Paraguai pelo fitoplâncton, perifíton, vegetação herbácea e bosques fluviais é analisado comparativamente. Esta síntese apresenta dificuldades relacionadas com a natureza dos subsistemas produtivos e com as escalas espaciais e temporais em que foram tomadas as informações.

Para comparar os sistemas produtivos destes rios, foram considerados não só os valores absolutos, mas também características tais como: permanência do aporte de matéria orgânica, qualidade do recurso, acessibilidade trófica, tempo de organização e tempo de resposta, mecanismos homeostáticos e transferência trófica.

De acordo com a dinâmica hidro-sedimentológica, se distinguem duas fases: "limnociclo", quando os limnótopos da planície de inundação estão isolados das águas correntes e "potamociclo", correspondendo ao período de inundação, com mudanças drásticas na estrutura biótica.

A produtividade do fitoplâncton dos corpos d'água

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da várzea é claramente diferente em ambas as fases consideradas, com altos valores no limnociclo, embora sejam discutidas as limitações metodológicas das estimativas.

Variações temporais no perifíton são elevadas e dependem essencialmente da velocidade da corrente em charcos e lagoas durante as inundações, da perda de vegetação e da turbidez produzida pela entrada de sólidos suspensos inorgânicos produzidos pelo rio.

É possível observar pelo menos cinco grupos ecológicos de macrófitas aquáticas no Baixo Paraná e no Baixo Paraguai, de acordo com as condições de produtividade e de transferência a outros níveis tróficos. A produtividade destas plantas é geralmente maior do que a do fitoplâncton e do perifíton.

A vegetação herbácea apresenta uma forte resposta à hidrodinâmica do rio. No início do potamociclo, durante os 10 ou 15 dias em que as plantas permanecem completamente submersas pelas águas da inundação, a taxa diária de produção pode ser de 3 a 10 vezes maior do que durante o resto do ano. Uma forte relação pode ser observada entre o nível hidrométrico e a produtividade, embora as diferentes espécies apresentem capacidades de respostas distintas.

Nas seções do Baixo Paraná e Baixo Paraguai, os bosques representam o sub-sistema de maior contribuição à produtividade primária líquida anual. É preciso destacar que a contribuição de matéria orgânica pelos bosques inundáveis não pode ser considerada como contribuição alóctone.

Nos estudos de rios de planície, a produtividade deve ser avaliada incluindo avaliações anuais dos sub-sistemas produtivos que interatuam com o fluxo de escoamento, tomando, retendo e liberando elementos transportados pelo rio. Funcionalmente, toda a produção primária ocorre na planície de inundação, dependendo do regime hidro-sedimentológico.

ABSTRACT - ASPECTS OF PRIMARY PRODUCTIVITY IN THE LOWER PARANA AND PARAGUAY RIVERINE SYSTEM

The organic matter supply to the Lower Paraná and Paraguay riverine system by the phytoplankton, periphyton, herbaceous macrophytes and the gallery forest are compared. This synthesis confronts difficulties related to the nature of productivity subsystems and river space-time scales.

In order to compare the productive subsystems of these rivers, many features are considered in addition to absolute values: permanence of the organic matter supply, quality of the source, trophic accessibility, time of organization and time of response, homeostatic mechanisms, and trophic transference.

According to the hydrosedimentological dynamic, two phases can be distinguished: "limnocycle", when the limnotopes of the floodplain are isolated from the running waters; and "potamocycle", corresponding to the flood period with drastic changes in biotic structure.

The phytoplankton productivity of the water bodies is clearly different in both phases, having high values in the limnocycle; although many methodological limitations are discussed.

Temporal fluctuation of the periphyton is high and depends essentially on the current velocity in pools and ponds during floods, on the loss of vegetation and the turbidity produced by the input of suspended inorganic solids brought by the river.

It is possible to observe at least five ecological groups of macrophytes in the Lower Paraná and Paraguay Rivers, according to conditions of productivity and transference to other trophic levels. The productivity of macrophytes is generally greater than that of phytoplankton and periphyton.

The herbaceous vegetation has a fast response to

the tiver hydrodynamic; during 10 to 15 days that plants remain completely submerged in the flood waters at the beggining of the potamocycle the daily productivity rate can be from three to ten times greater than during the rest of the year. A closed relationship between the hydrometric level and productivity can be observed, although different species have different reply capacities.

In the lower sections of the Paraguay and Paraná, the forest represents the subsystem of greatest net annual productivity. The organic matter supplied by flooded forest in these great rivers cannot be considered an allocthonous input.

In these floodplain rivers, evaluations of productivity must include the crops obtained for productive subsystems which interact with the flow, taking, retaining, and delivering elements transported by the river. Functionally, all the production is generated in the fluvial valley depending on the hydro-sedimentological regime and, in its turn, partakes in the general metabolism of the system.

INTRODUCTION

The object of this paper is to compare the organic matter supply to the Lower Paraná and Paraguay riverine system (Fig. 1) by different photosynthetic subsystems of the section subject to flooding, with special emphasis on phytoplankton, periphyton, herbaceous macrophytes and the plants of the gallery forest, based on information available.

This synthesis confronted many difficulties, such as:

- information published by several authors has been produced at different times and using different techniques;

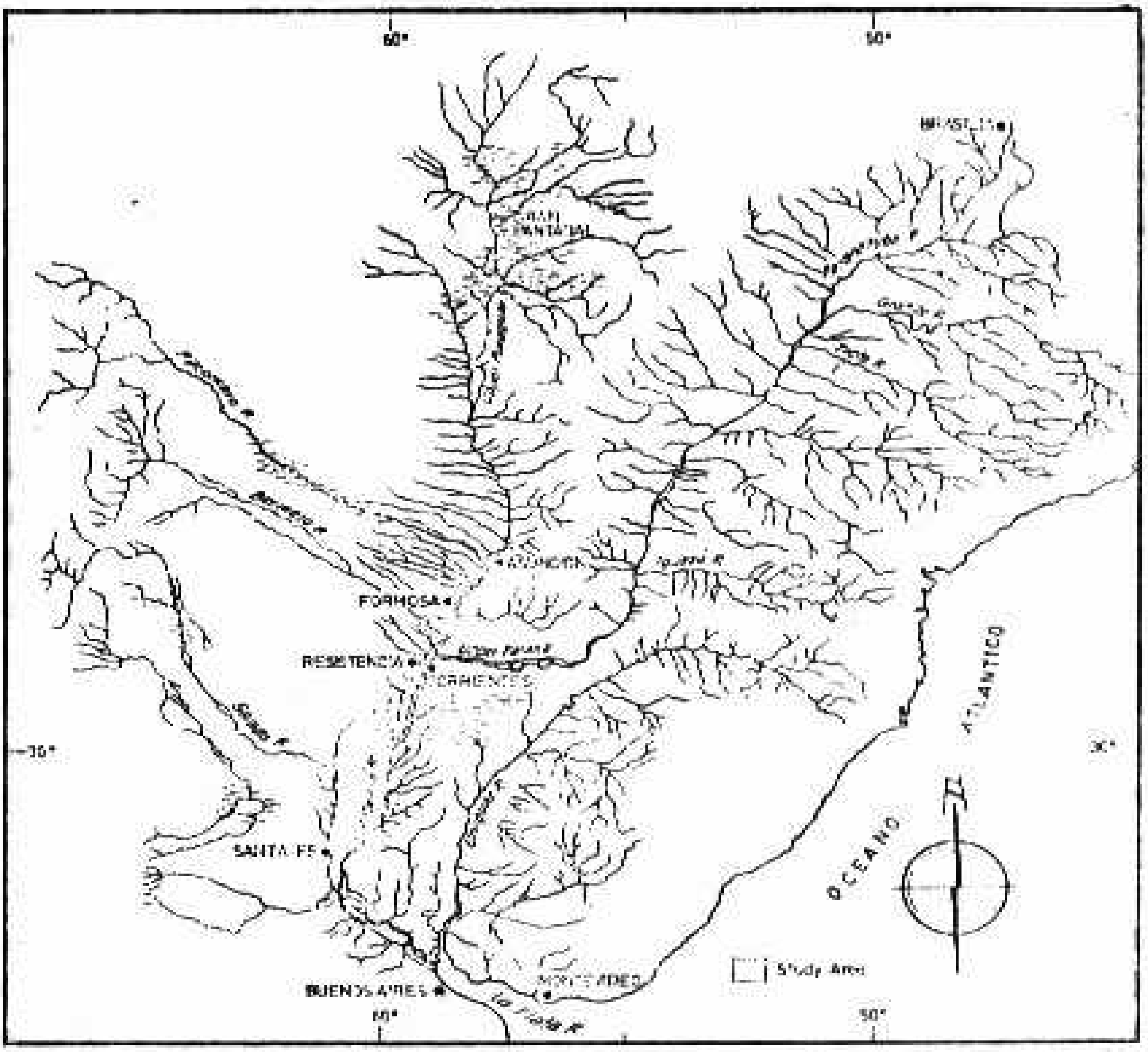

Figure 1 - The Parana-Paraguay basin.

- sampling units and methods of expressing data about productive system are structurally different, such as those used for phytoplankton and forests. Obviously, comparisons are not easy;

- the environmental complex that regulates the productivity of the subsystems of a riverine system is qualitatively and quantitatively different in space and time. Therefore, the results available can be considered as taken only at certain points and not always useful to this particular objective.

Even with these considerations in mind, it is useful to compare productivity of different units of a riverine environment and/or types of vegetation, in order to evaluate the organic matter supply to the metabolism of waters, to within an order of magnitude.

Important articles have been written (WESTLAKE, 1965; RODIN & BAZILEVICH, 1967; LIKENS, 1975; TUNDISI & TUNDISI, 1976) that permit a comparison of the productivity of the most prominent ecosystems of the world. Despite this, information about riverine environments is decidedly deficient. This lack is mainly ascrikable to difficulties of method and operation already mentioned, and to great variability in space and time of the large rivers.

When the productive subsystems of these rivers are compared the following characteristics should be kept in mind in addition to the absolute values:

a) PERMANENCE or continuity of the organic matter supply in the hydrologic cycle. The range of values is very great in the subsystems considered, with a pattern of seasonal variability in lakes isolated for long periods brought about by the fluvial hydrodynamics; although the dominant pattern of variability in levels of plankton production and vascular vegetation corresponds to the hydrosedimentological dynamics of the river, as will be mentioned later.

This means that the cause of the greatest changes arises from the climatic stimuli occuring in the headwaters of the river basins. The transmission of these stimuli, that appear as changes in the hydrometric state and the sedimentary load, are more gradual in the Paraguay River than in the Paraná (Fig. 2), due to the physiographic characteristics of the upper sections of the basins (SOLDANO, 1947).

Figure 2 - Hydrologic regime of Paraguay River (at Formosa city) and Parana River (at Corrientes city).

The permanence and regularity of the organic matter supply for productive subsystems largely qualifies the possibility of development of specialized trophic networks.

b) QUALITY OF THE RESOURCE. The presence of hard tissue and an unfavorable relation between carbon and nitrogen can in great measure produce different effects on the metabolism of bodies and courses of water (ESTEVES & CAMARGO, 1986).

c) Trophic ACCESSIBILITY of the resource, that is largely determined in point b), but is also related to the size of cells in the case of phytoplankton and with the nature of the litter fallen in forests.

As RAI (1982) has pointed out, the potentially transferable productivity of phytoplankton is concentrated mainly in nanoplankton. Then, it is indispensable to establish the supply of the component fractions of phytoplankton in all studies.

d) TIME OF ORGANIZATION AND TIME OF RESPONSE which are completely different in the productive subsystems considered. Phytoplankton must be measured by hours, hydrophytes by days, marsh vegetation by months, while fluvial forest can require years and decades. So, the organic matter supply between two high floods has fewer possibilities of recovery in forests than in plankton, where the persistence of the elements is lower.

e) REGULATING MECHANISMS of communities are completely different in the above mentioned subsystems:

- primary cellular productivity is supported by a high turnover rate, nutrients entering the population as a result of hydrosedimentological fluctuations, bringing about immediate changes.

- primary herbaceous productivity is also strongly linked to a river's hydrodynamics, although there are gradual changes in the dominant bioforms (NEIFF, 1975, 1979) and readjustments are a little slower, except in the floating vegetation of pools (POI de NEIFF & NEIFF, 1984).

- primary forest productivity of the valley is supported by euryoecious vegetation (NEIFF et alii, 1985; NEIFF, 1986a; REBORATTI & NEIFF, 1987) that constitute communities with a lower turnover rate in the proportionality of species. This subsystem is strongly affected during extraordinary floods (NEIFF et alii, 1985) by processes of erosion and accretion in the active plain of the river (BRINSON et alii, 1981) and also by the inundation times of the soil (NEIFF, 1986a).

Obviously, in order to explain changes in productivity of several subsystems, it is fundamentally important to know the frequency, quantity and persistence of the elements that affect it. Once this information is available (NEIFF, 1986b) it is possible to define the present state (tension or repose) and to anticipate the magnitude of changes in productivity, which may alter the normal pattern of subtropical rivers (NEIFF & POI de NEIFF, 1987).

f) TRANSFERENCE. Unfortunately, there is little or no information about the quantity and means by which the primary fluvial productivity is assimilated by animals of these rivers.

In communities of macrophytes, the amount and activity of the herbivores is low. Direct use of the marsh plants and the leaves of riverine forest can be considered scarce. The relation between animal and vegetable biomass in the pleuston of ponds the floodplain usually is 1:100 or even more different (POI de NEIFF & NEIFF, 1977; NEIFF & POI de NEIFF, 1984).

The little information available (POI de NEIFF & NEIFF (in press); BRUQUETAS de ZOZAYA & NEIFF (in press)) shows that colonization of the litter of aquatic and marsh plants by shredders is very low.

The biggest part of this primary productivity of the riverine system is metabolized by organisms that collect debris (collectors) (POI de NEIFF & NEIFF (in press)).

PRODUCTIVITY OF THE PHYTOPLANKTON

The information available about productivity of phytoplankton (Tab. 1) has been obtained by the classical method of clear and dark bottles, by successive estimates of dissolved oxygen and/or radioactive carbon, in the field and/or the laboratory. This method is generally accepted in marine and lacustrine studies (PETERSON, 1985). It has not been sufficiently discussed in estimates for muddy running water, rich in inorganic compounds, like the great

Table 1 - Phytoplankton net productivity of some rivers and floodplain lakes.

	River System	Productivity		Authority
	Amazon river			
	-Castanho lake (white water)	0.35 -1.50	($gC.m^{-2}.d^{-1}$)	FITTKAU et alii (1975)
	- Cristalino lake (black water)	0.05 -1.04	"	RAI & HILL (1984)
	-Redondo lake	0.29	"	MARLIER (1967)
	-Negro river (black water)	0.06	"	SCHMIDT (1976)
	-Tapajos river	0.44 -2.41	"	SCHMIDT (1982)*
(F)	Paraguay river			
	-Herradura	0.08 -1.25	"	BONETTO, C. (1982)
	-Puerto Bermejo	0.004-0.06	"	BONETTO, C. (1982)
	-Paraguay Lower	0.060-0.750	"	BONETTO, C. et alii (1981)
	-Herradura pond	0.01 -0.45	"	ZALOCAR et alii (1982)
	Paraná river			
(F)	-Upper Paraná (Itá Ibaté City)	0.002-0.99	"	BONETTO, C. (1982)
(L)	-Lower Paraná (Paraná City)	0.001-0.80	"	PEROTTI de JORDA (1984)
(F)	-Lower Paraná (Corrientes City) km 1208			
	. right bank	0.010-0.580	"	BONETTO, C. (1983)
	. left bank	0.003-0.285	"	BONETTO, C. (1983)
(F)	- Lower Paraná (Corrientes City) km 1208			
	. right bank	0.000-0.120	"	BONETTO, C. et alii (1979)
	. left bank	0.003-0.285	"	BONETTO, C. et alii (1979)
(F)	-Lower Paraná (Esquina City)	0.030-0.850	"	BONETTO, C. (1983)
(L)	-Lower Paraná (Corrientes City)	0.041	($mgC.m^{-3}.h^{-1}$)	PEROTTI de JORDA (1980a,b)
(L)	-Lower Paraná (Bella Vista City) km 1060	0.041	"	PEROTTI de JORDA (1980a,b)
(L)	-Lower Paraná (km 876)	0.045	"	PEROTTI de JORDA (1980a,b)
(L)	-Lower Paraná (Diamante City)	0.195	"	PEROTTI de JORDA (1980a,b)

Note: (F) = field experiment (in situ)
(L) = laboratory experiment
* = from WELCOMME (1985)

floodplain rivers of South America. In addition to the interference that these environmental conditions can generate, a measurement obtained by isolating running water of the river for a long time seems questionable; i.e., the method transforms an open system into another completely closed and static one. Recent studies seem to indicate a deficiency of phosphorus in the nutritional balance of the Upper Paraná (N/P = 35) and of nitrogen in the Paraguay-Bermejo axis (N/P = 6) (BONETTO (in press)), that can become limiting to productivity of phytoplankton in prolonged incubations. In view of these doubts it would be prudent to use the information from these estimates with reserve.

From Tab. 1 a clear asymmetry can be inferred between magnitudes of productivity belonging to the drainage axis, and measurements taken in lakes or ponds subject to flooding from these great rivers (GARCÍA de EMILIANI & ANSELMI de MANAVELLA, 1983). Undoubtedly, lentic conditions are more favourable for planktonic primary productivity, not only because of a reduced water flow, but also due to the lessening of turbidity.

The papers referring to the Paraná and Paraguay Rivers in Tab. 1, agree in point out that the main limiting factor for productivity is the turbidity, although the enrichment of water from the Paraguay-Bermejo axis with nitrogen, and those of the High Paraná with phosphorus has produced significant increase in productivity biotests in the laboratory (BONETTO, 1982).

The P:N ratio in the Paraguay and Paraná might become a factor of greater importance in man-made lakes of these rivers, as phytoplankton increase due to the increase of transparency (BONETTO (in press)).

The phytoplankton biomass of the Paraná has a low chlorophyll concentration (2.8-17.3 mg/Cl$\underline{a}$/m^3) (PEROTTI de JORDA, 1984), even comparable to mountain rivers (ARUGA & MONSI, 1963).

Values in Tab. 1 indicate that planktonic primary productivity of the Lower Paraguay and Paraná rivers is lower than other great warm rivers of South America.

The productivity of running water of these rivers fluctuates greatly in relation to fluvial hydrodynamics (PEROTTI de JORDA, 1977 and 1984; BONETTO, 1983); the higher values have been found during the low water phase (PEROTTI de JORDA, 1982).

Samples taken at certain points along the length of the Paraná River lead one to suppose that the chlorophyll concentration and planktonic productivity increase downstream (PEROTTI de JORDA, 1984). However, this observation may have operative limitations, and it might have resulted from an increase of hydrometric changes that took place during the sampling period.

That a gradient of planktonic productivity, such as that found by GREEMBERG (1964) in California should exist in the Paraná, does not seem clear, and if it were so, it could be more related to an increase in the quality of the limnotopes and to the greater extension that they occupy in the valley, than to the enrichment of the plankton with elements in the upper reaches of the river.

That is to say, that the quali-quantitative increase of plankton in the lower sections of the Paraná should be studied through mesologic changes caused by:

a) Enrichment (quality and quantity) of limnotopes.

b) The discontinuity (matter and energy) that affects the river from its concluence with the Paraguay River. At this point the Paraná increase its volume of water by one fourth, and its solid load by up to 70%. Thus, a frontier is formed which clearly defines two subsystems: the Lower and Upper Paraná River (NEIFF, 1986b).

The quali-quantitative increase of the plankton downstream from the Paraná-Paraguay confluence would not fit the pattern of planktonic development proposed by

Talling (RZÓSKA, 1978), as the changes downstream are a product of the physical-chemical discontinuity of the riverine system.

In the ponds of the flood valley there is a clear contrast between the low potamocycle productivity values and those obtained in the limnocycle, when they are isolated from the influence of the river (PEROTTI de JORDA, 1977; BONETTO, 1982). Therefore, the annual productivity greatly depends on the duration of both phases.

Thus, planktonic primary productivity is a quantitatively low, discontinuous and unpredictable supply for organisms which depend on it.

PRIMARY PRODUCTIVITY OF PERIPHYTON

There is no information published regarding the Paraguay basin and that available for the Paraná River is limited to the lower section. Studies performed may be considered as insufficient and with limited use for estimating levels of absolute values.

It is evident that periphyton does not has a continuous energetic supply in space and time (RAI & HILL, 1984). Its development is strongly influenced by the flow velocity (TRAAEN & LINDSTRØN, 1983), through its permanence is limited in water bodies within the islands and flood valley. In these environments it depends largely on the vegetation type (floating, rooted, emergent) and on the light interference that is proportional to the density of plants.

Temporal fluctuations are high and depend essentially on the current velocity in ponds during floods, on the loss of vegetation and the turbidity produced by suspended inorganic solids brought by the river.

The productivity of periphyton in the Paraná River could be lower than that of other great South American rivers. APESTEGUÍA & MARTA (1979) provide maximum value of 0.141 $mgC.dm^{-2}.d^{-1}$ and 0.315 $mgC.dm^{-2}.d^{-1}$ for coastal areas of the Correntoso River, a tributary of the Lower Paraná.

In La Cuarentena pond connected temporarily to the main course of the Lower Paraná, SACHI (1983) made an estimate of 1.27 $mgC.dm^{-2}.d^{-1}$.

In lakes of the central area of the Amazon, RAI & HILL (1984) estimated that productivity of periphyton is 7.46 $mgC.m^{-2}.d^{-1}$ and that it would correspond to an annual productivity greater than 20 $tmC.ha^{-1}.year^{-1}$.

RAI & HILL (1984), established a closed dependence of periphyton in relation to the hydrometric fluctuations, with maximum values of 24 $gC.m^{-2}.d^{-1}$ when Cristalino Lake had a high level of water.

According to MIKKOLA & ARIAS (1976) and DUCHARME (1975), periphyton is more productive than phytoplankton in the marshes of the Magdalena River.

It is possible that periphyton in the Lower Paraguay and Paraná has a greater productivity than that observed by APESTEGUÍA & MARTA (1979), because this estimate was performed using glass tubes. Therefore, absolute values are not reliable even though relative values can be used to determine the variation range (WETZEL, 1983).

This might be an important resource in the nutrition of other organisms, considering the extension of the valley and the covering of vegetation in the Paraguay and Paraná floodplain. BOWEN (1979) established that in a warm lake in Venezuela (Lake Valencia) periphyton constituted 42% of the organic matter, even though the algae only provided 0.2 to 2.8% of the periphytic detrital aggregate (PDA) dry weight.

PRIMARY PRODUCTIVITY OF THE FLUVIAL FOREST

There is little information about productivity of forest subject to flooding in the Lower Paraguay and Paraná (NEIFF & REBORATTI (in press)), even though they represent one of the subsystems which supply the greatest quantities of organic matter to the aquatic environment. Organic matter supplied by forests subject to flood in the floodplains of the great rivers cannot be considered an alloctonous supply as has been widely published in bibliography referring to vegetated streams of temperate areas. The origin, structure and productivity of these forests are strongly conditioned by the hydrodynamics of the river. They interact, taking up, retainin and delivering nutrients in close relation to hydrosedimentological phases.

In the lower sections of the Paraguay River, they occupy a greater relative surface than in the Lower Paraná River. From Puerto Pilcomayo up to the mouth of the Paraguay River, the gallery forest subject to flood covers approximately 39.000 hectares, while herbaceous wetlands cover 14.500 hectares, permanent water bodies (ponds and oxbow-labes) 17.000 hectares and the river course water about 23.200 hectares. The surface of the forests increases towards the mouth of the Paraguay River in the Paraná (NEIFF et alii, 1985). The Bermejo as well as about 30 Chaco autochthon rivers which receive the supply from about 42.000 hectares of flood forests, flow into the Lower Paraná.

Downstream from the confluence with the Paraguay River, in the Lower Paraná, the surface of forests decreases, occupying a relatively smaller surface than that of the herbaceous wetlands. In this section, forests are quali-quantitatively more heterogeneous and only those trees (*Tessaria integrifolia* forest) occupy more than 30.000 hectares (REBORATTI & NEIFF, 1987).

Among the riverine systems considered, forests represent the subsystem of greatest net annual productivity. In stands of *Tessaria integrifolia* near the Paraná-Paraguay confluence, the most frequent estimates showed values of 24-36 tm/ha/year (NEIFF & REBORATTI, 1985). The supply of organic matter of these forests enters the riverine system principally through four "compartments":

a) Incorporation of great surfaces of forest to the basin of the river during the floods by erosion of banks.

b) Seasonal falling of leaves, flowers, fruits and small twigs due to normal change of foliage (litterfall).

c) Defoliation of the plant stratum which remains submerged during very prolonged flooding.

d) Incorporation of organic matter by roots into the soil.

The supply of the first compartment is important during extraordinary floods and provides evidence that the biotic system has been completely surpassed in its capacity to reply. It is very difficult to evaluate the amount of organic matter included in landslides, because it depends largely on the magnitude of floods and the forest type considered.

During a period of extraordinary flood (1978-1983) 45-70% of forests in the lower section of the Paraguay River were killed (NEIFF et alii, 1985). The estimate of biomass of *Tessaria integrifolia* forest in this section was about 100 tm/ha (NEIFF, 1985) and approximately 120 tm/ha for so-called "monte negro" (pluristratified, plurispecific forest).

This supply of organic matter is not well incorporated into the metabolism of the river, and it produces important changes in the morphogenesis of islands, and it favours the increase and the obturation of secondary river branches.

The supply of organic matter due to the seasonal change of foliage is very important as the tissues are soft and easily degraded and are incorporated into the metabolism of waters. The estimates made in *Tessaria integrifolia* forests at the Paraná-Paraguay confluence show the following values of dry organic matter:

- 6.3 tm/ha for year 1979
- 12.2 tm/ha for 1982
- 7.2 tm/ha for 1984

Monthly and annual fluctuations depend largely on the hydrodynamics of the river (NEIFF, 1985). During periods of hydric stress, the foliar abscission increases (NEIFF & POI de NEIFF (in press)).

The contribution of organic matter by litterfall is only comparable in quantity with the production of certain floating and marsh species that grow in the flood valley.

During floods, the pioneer forest of *Salix humboldtiana*, *Tessaria integrifolia* and other species which grow on low islands of the basin, remain submerged for a long time, then undergoes foliar abscission. In stands 2 m high, with a density greater than 100.000 plants/ha, the values estimated were 0.9 to 1.6 tm/ha. When the river waters descend, plants can bud once more, so the foliar structures are reorganized.

Although in the Paraná and Paraguay Rivers the falling of leaves is closely related to hydric seasonality in the same way as in the Amazon (FRANKEN et alii, 1979), the supply of dead leaves is greater than the estimates performed there.

ADIS et alii (1979) provide data about the dynamics of liberation of nutrients in the litter of the Amazon flooded forest. They noticed a close relationship with hydrodynamics of the river and estimated that the mineral content is approximately 0.27 tm/ha/year.

In forests of *T. integrifolia* near the Paraná-Paraguay confluence, the percentage of ashes is between 11 and 14% of the dry weight of dead leaves. This relation makes it possible to estimate the supply of total minerals (ashes) as follow:

- 0.690 to 0.882 tn/ha/year for 1979
- 1.342 to 1.708 tn/ha/year for 1982
- 0.792 to 1.008 tn/ha/year for 1984

According to the analysis performed by LANCELE (pers. comm.) the following values of Na, K, Ca and Mg were present in the ashes:

Sample	% digested (mg)	% Na	% K	% Ca	% Mg
A	94.4	3.7	12.7	15.9	1.3
B	95.6	7.8	16.3	3.7	1.0
C	97.0	3.6	16.5	15.5	2.1

These concentrations are considerably greater than those found in the litter of the Amazon flooded forest (ADIS et alii, 1979), which could be related to the greater supply of nutrients in the islands of Paraná-Paraguay.

PRODUCTIVITY OF MACROPHYTES

Tab. 2 presents the comparative data of productivity of aquatic herbaceous vegetation in warm climate ecosystems.

A great range of values is noticeable among different types of vegetation (bioforms) and also among geographic areas, although productivity per unit of surface could be greater like phytoplankton and periphyton ones.

In the Lower Paraná and Paraguay during different hydrologic phases, it is possible to observe at least five different ecological groups according to conditions of transference of production to other trophic levels (Tab. 2).

Group A: corresponds to free-floating plants.

Table 2 - Net primary productivity (NPP) of macrophytes in floodplain of the lower Paraguay-Paraná system and other tropical wetlands.

Specie	Group	Place	Year	Authority	NPP ($tn.ha^{-1}.año^{-1}$)
Eichhornia crassipes		PNA-Barranqueras pond	1977	NEIFF y POI de NEIFF (1984)	12.46
Eichhornia crassipes	A_1	PNA-Santa Fe		LALLANA (1980)	13.80
Eichhornia crassipes		India	1971	GOPAL (1973)	6.75
Eichhornia crassipes		India		SAHAI y SINHA (1970)	2.71
Pistia stratiotes		PNA-Barranqueras pond	1976	POI de NEIFF y NEIFF (1977)	1.50
Azolla caroliniana	A_2	PNA-Santa Fe-Antequeras	1971/84	NEIFF y POI de NEIFF (1983)	2.56
Azolla pinnata		India		GOPAL (1973)	2.80
Salvinia herzogii		PNA-Southeast Chaco	1979/80	NEIFF y POI de NEIFF (1983)	1.67
Nymphoides indica		Represa do Lobo-S.Paulo	1984	MENEZES (1984)*	4.41-10.69
Nymphoides indica		PNA-Santa Fe-Corrientes	1971/82	NEIFF y POI de NEIFF (1983)	0.8-2.2
Nymphaea amazonica	B	PNA-Corrientes (Iberá)	1977/78	NEIFF y POI de NEIFF (1983)	1.1-2.6
Victoria cruziana		PNA-Barranqueras	1977/78	NEIFF y POI de NEIFF (1983)	1.6-2.3
Typha latifolia		PGUY-Chaco-Formosa	1984/86	NEIFF (1986a)	14-23
Typha latifolia		PNA-Corrientes	1977/78	NEIFF (1986a)	15-19.5
Typha dominguensis		Africa		THOMPSON (1976)	22.88
Typha dominguensis	C	Africa		HOWARD-WILLIAMS y LENTON (1975)	15.00
Cyperus giganteus		PNA-Chaco	1980	NEIFF (1986b)	12-20
Cyperus papirus		White Nile		PEARSALL (1959)	46-70
Paspalum repens		PNA-Isla Choui		NEIFF (this study)	8.5-17
Panicum elephantipes	D	PNA-Isla Choui		NEIFF (this study)	7-13
Panicum grumosum		PNA-Isla Choui		NEIFF (this study)	7-16
Polygonum acuminatum		PGUY - various islands	1980/86	NEIFF (this study)	12.5-19
Hymenachne amplexicaulis		PNA-Southeast Chaco	1979/80	NEIFF (1980, 1982)	16-21
Echinochloa polystachya		PNA-Southeast Chaco	1979/80	NEIFF (1980)	4-6
Cynodon dactylon	E			HEEG & BREEN (1982)	8.39
Paspalum repens		Amazon		JUNK (1970)	3-5
Oriza sativa		India		GOPAL (1973)	12.5

Note: PNA = Lower Paraná Floodplain
PGUY = Lower Paraguay Valley
* = ESTEVES, F.A. (1988)

A_1: (only includes *Eichhornia crassipes*). The vegetation can develop and produce with relative independence from the hydrometric fluctuations. However, it only thrives in permanent aquatic environments and is replaced by vegetation of groups D and E during very low levels of the river (NEIFF, 1979).

It presents the greatest productivity registered in the whole valley of Paraguay and Paraná Rivers (PEREZ del VISO et alii, 1968; LALLANA, 1980; NEIFF E POI de NEIFF, 1984), although transference to other trophic levels is very low (NEIFF & POI de NEIFF, 1984); most of the organic matter produced is transfered to the limnobios by decomposition of litter (ESTEVES, 1981; ESTEVES & BARBIERI, 1983; ESTEVES & CAMARGO, 1986; POI de NEIFF and NEIFF, in press).

When we compare the *Eichhornia crassipes* biomass in the Paraná system (as a rough estimation of potential productivity) the follow values are availables:

	Range (dry wt.g.m^{-2})	Place	Authority
UPPER PARANA	689-1638	Six reservoirs in the Paranapanema and Upper Paraná	ESTEVES (1982
UPPER PARANA	510-900	Paraíba River	ALMEIDA ROCHA (1975)
UPPER PARANA	650-750	Tupicuá Dam	NEIFF & POI de NEIFF (1987)
LOWER PARANA	800-3200	Barranqueras Pond (Chaco)	POI de NEIFF et alii (1977)
LOWER PARANA	860-2332	Barranqueras Pond (Chaco)	NEIFF & POI de NEIFF (1984)
LOWER PARANA	1020-2213	La Tina Pond (Santa Fe)	LALLANA (1980)
LOWER PARANA	1100-1700	Several ponds (Santa Fe)	PEREZ del VISO et alii (1968)

Its possible that the lower biomass of *E. crassipes* in the Upper Paraná are related with the nutrient availability. We can think that the N and P input from the Paraguay-Bermejo system let a better growth of *E. crassipes*.

A_2: includes free-floating bioforms which normally colonize semipermanent pools and ponds. They grow rapidly after the pools have been formed by rains or flooding of the valley (NEIFF, 1979; NEIFF & POI de NEIFF, 1979; POI de NEIFF & NEIFF, 1977, 1984).

Although they have a low biomass per unit of surface and volume, the turnover rate is high (POI de NEIFF & NEIFF, 1977, 1984; NEIFF, 1982). When pools in the flood valley remain full of water for a year or more, microsuccessions are produced (POI de NEIFF & NEIFF, 1984) which cumminate in colonization by *Eichhornia crassipes* (NEIFF & POI de NEIFF, 1979). In permanent waters, this successional process continues with formation of sudds (SCHULZ, 1961; TUR, 1972) with an enrichment of the bioforms.

This successional process at the level of floating vegetation involves an increased accumulation of dead phytomass (NEIFF, 1982) and the decomposition rate is low, due to depletion of oxygen (POI de NEIFF & NEIFF (in press)).

Group B: includes macrophytes that only live in lakes with permanent waters. They rarely tolerate periods of extraordinary flooding (NEIFF, 1979) and die when the depth of the lake is greater than 4 m. They have soft tissues and root rapidly in the aquatic environment. Their net productivity in the Paraná lower valley was estimated at between 0.8 and 2.3 tn/ha/year.

Group C: helophytes that live in permanent or semi-permanent waters, in lakes and tropical swamps, with a low hydrometric fluctuation of basin of the tributaries of the Lower Paraguay and Paraná, and very rarely in islands of the flood valley (NEIFF, 1981, 1986a).

Consumption by herbivores and decomposition rate are very low (BRUQUETAS de ZOZAYA, 1986), therefore giving way to a process of filling of lakes with dead organic matter by formation of sudds (NEIFF, 1981). They produce enrichment with humic organic matter, which is very slowly recycled (HOWARD-WILLIAMS & HOWARD-WILLIAMS, 1978).

Thus, even with a high productivity, waterbodies dominated by this type of vegetation can be considered dystrophic (or saprotrophic) due to the slow transference of materials and energy, and its tendency to filling (NEIF, 1981).

Group D: These plants efficiently colonize banks of the streams and shores of sections of the main course of Paraguay and Paraná which have a moderate current and cover a large section of the flood plain as islands.

These plants of the rheophyton (NEIFF, 1986b) are tolerant to water level changes and to flow velocity.

This group gas a high productivity (SABATINI et alii, 1983) (Tab. 2) and the recycling is efficient because they are formed of soft tissues which are easily defraded by microorganisms. This process is also assisted by the greater availability of oxygen in these environments.

Group E: includes marsh hydrophytes that live in areas subject to flood in the Lower Paraguay and Paraná floodplains. Although these bioforms are very similar to those of group D, morphologically and physiologically, they are not very tolerant to the velocity of the flow, and live in areas of lower hydrometric fluctuation. They are characteristic of wetlands of outer banks of the flood valley and in shallow waters of floodplain rivers (JUNK, 1970).

The communities of groups D and E are used to feed fattening cattle as they form pastures of excellent quality.

The vegetable populations included in the groups mentioned above present a different adaptation to hydrometric fluctuations, and to the flow velocity.

Thus, the primary productivity of these rivers must be studied globally based on the information regarding reorganization of vegetation as a consequence of hydrologic phases of the river (NEIFF, 1975, 1979). It has been possible to establish satisfactorily the range of variability in systems with little regularity (NEIFF & POI de NEIFF, 1984).

In environments subject to flood it is not possible to distribute the samples isochronically as in the temperate climate lakes; the timetables of the samples must necessarily be irregular and adapted to the rhythm of hydrometric variability.

During the stress period of floods the productivity is very high (Tab. 3) plants must hasten their growth to reach the water surface (JUNK, 1973; NEIFF, 1979). During the 10 to 15 days that the plants remain completely submerged in the floodwaters, the daily productivity (Tab. 3) can be from three to ten times greater than during the rest of the year.

In Fig. 3 the close relationship between the hydrometric level and productivity can be observed, although the species have different reply capacities. In the emergent rooted plants, lower production can be observed after they have recovered from the stress of the flood.

There is much to be learned about the productivity of the Paraguay and Paraná rivers, to understand the productive dynamics of these riverine macrosystems.

The magnitude of the values registered for

Table 3 - Net primary productivity (dry weight) in the Paraná river floodplain, downstream from the Paraná-Paraguay confluence.

	Stress Period (days)	N.P.P. Stress Period ($Tn.ha^{-1}$)	N.P.P. Annual Period ($Tn.ha^{-1}.yr^{-1}$)	Production Rate ($g.m^{-2}.d^{-1}$)	N.P.P. Effective Annual ($Tn.ha^{-1}.yr^{-1}$)	Production Rate ($g.m^{-2}.d^{-1}$)	Site (*)	Year
Polygonum ferrugineus	14	2.50	65.18	17.85	18.30	5.10	El Gato (IS)	1987
Ludwigia peploides	11	1.96	65.04	17.81	6.7	1.84	La Guardia Santa Fe (BW)	1971
Victoria cruziana	10	0.29	10.58	2.90	0.89	0.24	Baupé (Chaco) (P)	1976
Nymphoides indica	10	0.85	31.02	8.50	2.20	0.60	Don Felipe Santa Fe	1971
Echinochloa polystachya	12	1.72	52.31	14.33	14.10	3.86	La Cacerola Santa Fe (P)	1971
		FLOOD PERIOD -POTAMOCYCLE-			LOW-WATER PERIOD -LIMNOCYCLE-			

References: (*)

P = Pond

BW = Backswamp

IS = Island

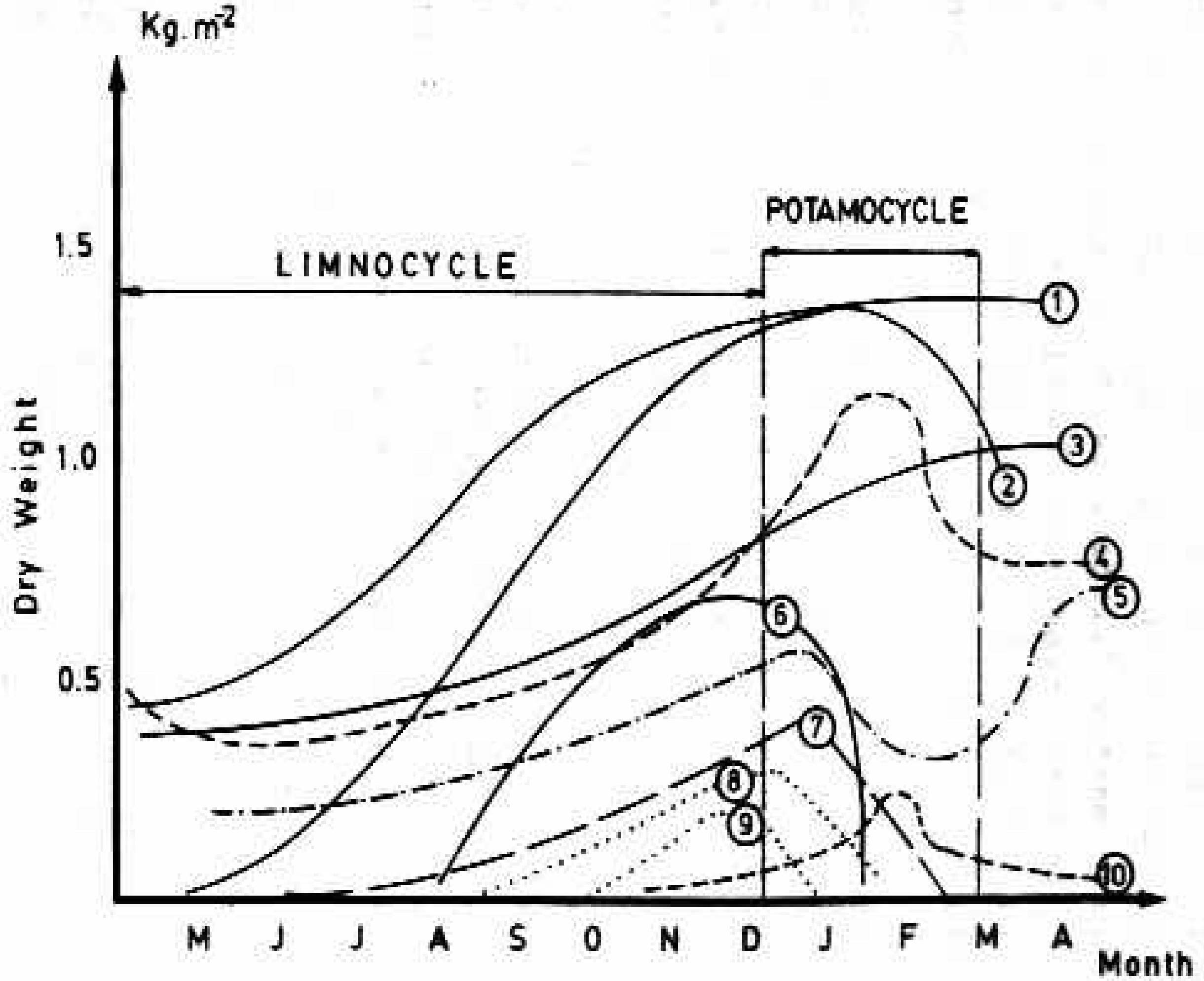

Figure 3 - Standing crop curves of several macrophytes near the Parná-Paraguay confluence.

1- *Eichhornia crassipes*	2- *Eichhornia azurea*
3- *Ludwigia peploides*	4- *Polygonum ferrugineus*
5- *Polygonun punctatum*	6- *Nymphoides indica*
7- *Myriophyllum brasiliense*	8- *Plagiocheillus tenacetoides*
9- *Hydrocotyle ranunculoides*	10- *Victoria cruziana*

different subsystems (phytoplankton, periphyton, macrophytes) shows a great temporal range, depending closely on the hydrosedimentological dynamics of the river.

On the other hand, from the main course to the higher section of the valley can be found clines of productivity with quali-quantitatively different vegetation biotopes, with different biomass production potential and with different turnover rates. In these PRODUCTIVE CLINES, the environment is more predictable for organisms in higher biotopes (less dependence on input from flooding) and the supply of organic matter (litter) is more permanent over time (Fig. 4). In these swamps and wetlands the constant availability of detritus allows the formation of trophic networks having considerable disparity between the biomass of primary producers and consumers.

In the main course of these rivers, cellular organisms have the principal role in productivity, partially adapted to a not very predicable environment, because there is great fluctuation between two hydrologic phases of the river and even more between different hydrologic cycles.

In the multiple productive subsystems of the Lower Paraguay and Paraná Rivers, the absolute productivity values available are similar or greater than those for homologous biotopes on "dry ground" (so called "tierra firme"). Although these wetlands and swamps of the flood valley are more variable temporally, the time of reply to the changes in the physical-chemical environment is less although reorganization capacity is greater in these open systems.

Evidently, in these floodplain rivers, productivity must be evaluated including the crops obtained for productive subsystems which interact with the flow, taking, retaining, and delivering elements transported by the river. Functionally, all production is generated in the fluvial valley depending on the hydrosedimentologic regime

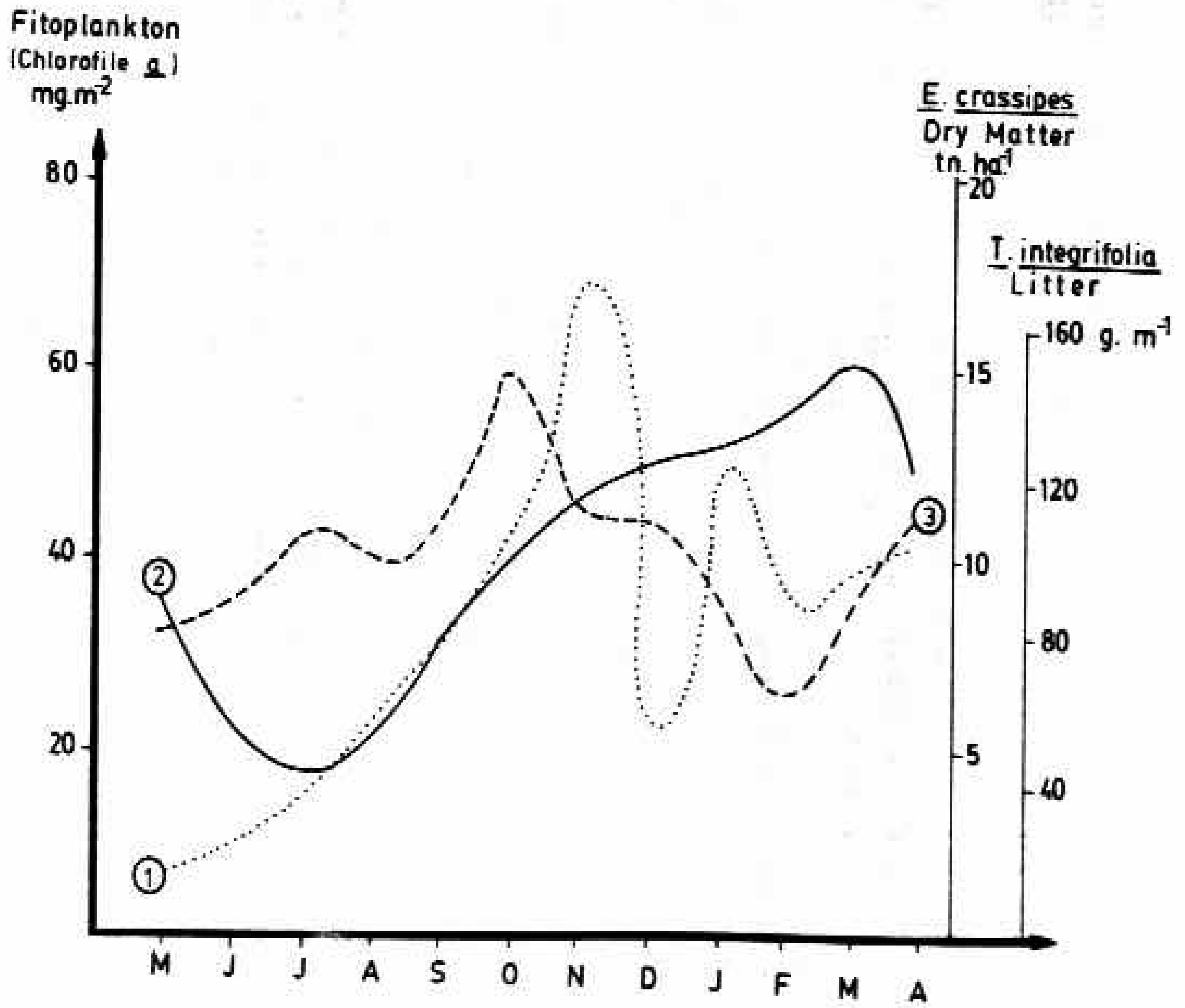

Figure 4 - Phytoplankton clorophyll a (after Perotti de Jorda, 1984) (1); Pleuston of *Eichhornia crassipes* (Neiff & Poi de Neiff, 1984) (2); Litter fall in *Tessaria integrifolia* floodplain forest (Neiff, 1985).

and, in its turn, partakes in the general metabolism of the system.

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