***OECOLOGIA BRASILIENSIS***
Esteves, F. A. 1998. Considerations on the ecology of wetlands, with emphasis on Brazilian floodplain ecosystems. pp. 111-135. **In** Scarano, F. R. & A.C. Franco (eds.). *Ecophysiological strategies of xerophytic and amphibious plants in the neotropics.* Series Oecologia Brasiliensis, vol. IV. PPGE-UFRJ. Rio de Janeiro, Brazil.

# CONSIDERATIONS ON THE ECOLOGY OF WETLANDS, WITH EMPHASIS ON BRAZILIAN FLOODPLAIN ECOSYSTEMS

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**Resumo:**

**"Considerações sobre a ecologia de áreas inundáveis, com ênfase nos ecossistemas das planícies inundáveis brasileiras."**

Este trabalho apresenta uma síntese dos principais aspectos da ecologia de áreas inundáveis, enfatizando sistemas brasileiros. Os problemas referentes à definição destas áreas são discutidos e são apresentadas considerações históricas acerca do seu uso pelo homem. Os fenômenos de inundação e seca são analisados num contexto ecológico como os principais agentes limitantes ao processo sucessional, que nestes ecossistemas é notavelmente mantido em suas fases iniciais. O papel da inundação e da seca como fatores de estresse ecológico para comunidades alagáveis também é discutido. Os organismos das áreas inundáveis brasileiras estão adaptados a diferentes graus de inundação e seca. Dentre as comunidades vegetais existem várias espécies r-estrategistas, caracterizadas por uma capacidade de produzir um grande número de propágulos e por suas altas taxas de produtividade primária a curto prazo. Especial atenção é dada ao sistema rio-planície de inundação, como um dos mais importantes sistemas inundáveis do Brasil. Discute-se o papel do pulso de inundação na dinâmica das comunidades destes sistemas, enfatizando especialmente comunidades vegetais (fitoplâncton, macrófitas aquáticas e florestas inundáveis).

**Abstract:**

This essay presents a synthesis of the main aspects of wetland ecology, emphasizing Brazilian systems. Problems regarding the definition of these areas are discussed, and historical considerations on their use by humans are presented. The phenomenon of flooding and drought is considered, in an ecological context, as the principal agent interrupting the successional process, which in these ecosystems is notably maintained in its initial stages. The role of flooding and drought as ecological stress factors for wetland communities is also discussed. In Brazilian wetlands, organisms are adapted at different levels to flood and drought conditions. Plant communities contain many r-strategist species, characterized by their capacity to produce many seeds and by their high rate of short-term primary productivity. Special attention is given to the river-floodplain system, as one of the most important wetland systems in Brazil. The role of the flood pulse in the community dynamics of these systems, emphasizing especially the plant communities (phytoplankton, aquatic macrophytes, and floodplain forest), is discussed.

## Wetlands and the Problem of Their Definition

Wetlands occupy approximately 6% of the land surface and are found in all regions of the world (Table 1). They constitute one of the most important ecosystems for man, although they are among the least well known scientifically. Only in recent decades have societies come to recognize the relevance of wetlands as a source of products and services of immense social and economic importance.

Table 1. Estimated extent of the world's wetlands (modified from Mitsch & Gosselink, 1993).

| Region | Area ($Km^2X1000$) | % of the Region's Area | % of the World's Wetlands |
|---|---|---|---|
| Polar | 200 | 2.5 | 2 |
| Boreal | 2558 | 11.0 | 30 |
| Subboreal | 1017 | 13.4 | 12 |
| Subtropical | 2145 | 29.3 | 25 |
| Tropical | 2638 | 10.9 | 31 |

Wetlands are important in flood control, aquifer replenishment, erosion and sedimentation control, and as habitats for many animal and plant species that are important to man. Much of the biota of Brazilian wetlands is still poorly understood scientifically, which makes it more difficult to label this type of ecosystem as an important reservoir of biodiversity. More recently, many authors have demonstrated the role of wetlands in the control of pollution, artificial eutrophication, and sanitary degradation of waterbodies. Among these are Kadlec & Knight (1996), whose treatise on wetlands includes the possibility of using these ecosystems to treat domestic and industrial effluents.

Heterogeneity in geographic distribution, hydrological regime, soil and water quality, and the types of plant and animal communities, make the definition of wetlands one of the most difficult exercises in ecology. Several authors, such as Cowardin *et al.* (1979) and Mitsch & Gosselink (1993), among others, have emphasized the need to seek a definition for each type of wetland, due to the difficulty of establishing a unifying definition for all types of areas subject to flooding.

The term "wetlands" (in Portuguese, "áreas alagáveis" or "áreas inundáveis") was initially used to characterize environments with permanently moist or flooded soils and characteristic vegetation, composed mainly of grass species, which ecologists term hydrophytes. The more general term includes "marshes", "swamps", and "bogs", the most intensely studied wetland types. From research in these environments, especially in temperate regions, arose some of the main concepts of modern ecology, including the trophic-dynamic concept developed by Lindemann (1942) during his pioneering researches in a small pond, Cedar Creek Bog, in the state of Minnesota, U.S.A.

A growing number of ecological research projects in wetlands, especially in subtropical and tropical regions, has shown that many wetlands in those regions have hydrological and ecological characteristics very different from those of temperate wetlands. In Europe and North America, from the 1960s onward, wetlands have suffered from intense manmade impacts, which led legislators and environmental control agencies in several countries to seek more precise definitions for these environments. From this necessity arose several definitions, such as:

1) North American definition (Cowardin *et al.*, 1979): "Wetlands are transitional zones between aquatic and terrestrial ecosystems, with the water level at or near the surface, or zones of shallow water. Wetlands must possess one or more of the three following attributes: a) hydrophytes must predominate, at least periodically; b) the soil must be predominantly poorly drained and hydromorphic; c) the soil must be saturated or covered by shallow water during some part of the growing season."

2) Canadian definition (Zoltai, 1979): "Wetlands are defined as zones where the water level is near or above the soil surface, or zones that are water-saturated for a period sufficient to permit the development of characteristics of wetlands or aquatic zones, such as: hydromorphic soils, hydrophytic vegetation, and various characteristic processes of aquatic environments."

3) International definition (Navid, 1989): The International Union for the Conservation of Nature and Natural Resources (IUCN) and the "Convention on Wetlands of International Importance, Especially as Waterfowl Habitat", better known as the Ramsar Convention, adopted the following definition: "Marshy areas, natural or artificial, with standing or flowing water, fresh, brackish, or saline, including marine, with depth not greater than 6 meters."

According to Mitsch & Gosselink (1993) no definition of wetlands completely satisfies the interests of both scientists and administrators. Different professionals (geologists, educators, hydrologists, ecologists, sociologists, economists, political scientists, lawyers, *etc.*) may propose different definitions for wetlands reflecting their different training and interests.

The above definitions plus others encountered in the literature, summarized by Cowardin *et al.* (1979) and Mitsch & Gosselink (1993), are not applicable to Brazilian wetlands, which in most cases have ecological characteristics much different from those in the temperate zone. Contrary to most Northern Hemisphere wetlands, in Brazil the most extensive wetlands are strongly linked to the dynamics of their associated rivers. Some Brazilian wetlands are among the largest in the world, particularly those associated with the Amazon, Paraná, Araguaia, and São Francisco rivers, among others.

The search for a definition of Brazilian wetlands must take into account one of the most characteristic features of these environments, the vegetation. This component shows adaptations for all types of Brazilian wetlands. Thus, Brazilian wetlands can be defined as zones where the colonizing vegetation is tolerant of or adapted to wet soils or to soils that undergo daily or seasonal flooding. It is necessary to point out, however, that more important than the search for an adequate definition is the necessity to increase scientific understanding of the structure and functioning of the ecosystems composing Brazilian wetlands. Without such understanding, no proposal for rational use, management, or recovery of Brazilian wetlands will be viable.

## Historical Considerations on Wetland Use

The history of human use of wetlands reprises the history of the human race. In this type of environment the first civilizations developed, such as those that arose and colonized over centuries the wetlands of the Nile, Euphrates, Tigris, Indus, Mekong, and other rivers. In these wetlands, the civilizations of that time obtained abundant resources indispensable to their survival, such as food crops produced in the fertile soils of these areas. Thus the socio-economic systems of these civilizations were linked to the characteristics of the supporting wetlands. For example, rates of taxation in ancient Egypt were adjusted according to the water levels of the Nile. In years of limited floods and reduced harvests, taxes were lowered. In years with extensive floods, agricultural production increased, and the government increased rates of taxation accordingly (Hammerton, 1972). In China, rice cultivation has been carried out in concert with fish production for millennia (Mitsch & Gosselink, 1993). According to Porro (1992), colonization of the Amazon region about 2,000 years ago occurred along the floodplains (*várzeas*), because of their high fertility.

In recent history, wetlands were considered, especially in the Occident, as dangerous and unhealthy places. As a consequence they attracted no economic interest, nor was their ecological value recognized. To illustrate this point, a number of expressions in various languages clearly indicate the rejection of wetlands by different cultures. For example, in English: "We get *bogged* down in detail" and "we are *swamped* with work" (Mitsch & Gosselink, 1993). According to these authors, many Hollywood films also propagated negative concepts of wetlands: "Creature from the Black Lagoon" (1954), "Swamp Thing" (1982), and "Return of the Swamp Thing" (1989).

Based on this erroneous view of wetlands, many such areas were destroyed. The most fantastic examples come from the Northern Hemisphere, where for example Mexico City, Chicago, and Washington, DC (USA) grew at the cost of nearly eliminating their wetlands (Mitsch & Gosselink, 1993). These authors aver that 27% of the area of the state of Illinois (USA) alone, equivalent to 40,000 km$^2$, consists of former wetlands now transformed into urban or agricultural lands. Several North American airports, including those of Boston, New Orleans and New York (J. F. Kennedy) were constructed on former wetlands.

In Brazil, the idea of wetlands as ill-omened, unhealthy environments still persists. In the name of public health, that is in order to "destroy" the *foci* of yellow fever and malaria in Rio de Janeiro state, the former Department of Public Works and Sanitation (Departamento de Obras e Saneamento, DNOS) drained and/or filled several wetlands in the capital and throughout the state. During that period, wetlands of considerable extent, especially in the northern lowlands were filled and urbanized. More recently, land speculation has become another factor contributing heavily to the degradation or even destruction of wetlands in several parts of Brazil, especially in the state of Rio de Janeiro. In the Barra da Tijuca neighborhood of the city of Rio de Janeiro, since 1970 nearly all the wetlands have been filled in for residential or commercial construction. In order to gain an idea of the view of wetlands in Brazil at that time, it is sufficient to call to mind the still current expression, "*a vaca foi para o brejo*" literally meaning "the cow went to the swamp", which is a strongly pejorative expression signifying utter failure of a project or initiative.

Certainly, the idea of unhealthy habitats, inappropriate for human use, was one of the chief reasons that many wetlands in Brazil remained ecologically intact until the beginning of the 1970s. Among these were the enormously extensive wetlands in Amazonia and the Pantanal of Mato Grosso. These wetlands were becoming more intensively settled at about the same time that environmental legislation and above all, the realization of their ecological, economic, and social importance had become reasonably well developed. However, enforcing the laws and perfecting the structure of environmental control are of fundamental importance in order to guarantee the ecological integrity of these environments.

## Flooding and Drying as Ecological Stressors on Wetlands

The succession of periodic flooding and drying events, typical of most wetlands, is an indispensable component in the maintenance and evolution of these environments. The species inhabiting wetlands were selected as a result of this kind of temporal variation in ecological conditions. The changes often found in ecological characteristics and in wetland communities are natural to these systems, as they occur within the normal limits of their ecological functioning.

In different wetland types, organisms are found with different levels of adaptation to ecological conditions. Some organisms are more adapted to aquatic conditions (flood phase) or more to terrestrial conditions (dry phase). The flood phase, while an ecological stressor, must be so considered only in relation to those species that are better adapted to terrestrial conditions, or to those terrestrial species that occupy the wetlands during the dry phase. The same consideration applies to the dry phase, which is a stressor for species that are more adapted to flood conditions.

However, extreme or prolonged floods and droughts must be considered as ecological stressors. These phenomena may occur sporadically and represent ecological stress to the extent that biological communities are not adapted to them. In both cases, the consequence of ecological stress is that some environmental factors exceed the functional limits of the species affected.

## Importance of Wetlands in the Carbon Cycle of the Biosphere

Although wetlands cover about $530 \times 10^6$ ha, corresponding to only 6.4% of the earth's surface (Mitsch & Gosselink, 1993), these environments play an important role in several processes of the biosphere. Among these processes is nutrient cycling, especially the carbon cycle.

The major importance of wetlands in the global carbon cycle is due principally to their high primary production, resulting in high carbon concentrations in the soils. From the mean carbon concentration in a 1 m profile of wetland soil, Schlesinger (1984) calculated a carbon stock of 72 kg/m$^2$, a very high value compared to other ecosystems. Based on this value, Schlesinger (1984) calculated the carbon stock in wetlands of the earth and arrived at a value of $180 \times 10^9$ tons of carbon, *i.e.* 12% of the total carbon in all the earth's soils. Based particularly on these results, the question arose as to the possibility that wetlands act as sinks or sources of carbon for the atmosphere. This question has not yet been answered. However, it can be inferred from the literature that different types of wetlands have different patterns of accumulating or liberating carbon into the atmosphere. In general, wetlands not impacted by human activities retain more carbon, especially in soils and vegetation.

The carbon cycle has been most intensely studied in wetlands formed by river-floodplain systems. According to Likens *et al.* (1981), $0.19 \times 10^9$ tons of carbon are deposited annually on the world's floodplains, and more than half of this carbon is liberated into the atmosphere. For Brazilian systems, the most applicable data were furnished by Junk (1985) for the Amazon River floodplain. According to this author, $1{,}535 \times 10^8$ tons of carbon are fixed annually on the Amazon river floodplain, 52% by herbaceous plants, 32% by floodplain forests, and 16% by phytoplankton. Of the total carbon, $4.7 \times 10^7$ tons annually are potentially available for export: 77% from floodplain forests, 21% from aquatic macrophytes, and 2% from phytoplankton. The actual amount exported is approximately $1.7 \times 10^7$ tons per year. According to Junk (1985), this demonstrates that the Amazon River floodplain is an exporter of carbon to the rivers of the region.

Calculations of carbon consumption by the aquatic macrophyte, *Echinochloa polystachya*, were performed by Piedade *et al.* (1992). According to these authors, this species covers an area of 5,000 km$^2$ on the Amazon floodplain, and its carbon consumption reaches $75 \times 10^6$ tons/year. On the floodplain, the incorporated carbon may have several destinies. A large part is liberated into the atmosphere through decomposition (*c.* 1,600 g/m$^2$/year), another part is exported to the Amazon basin, and a third part is incorporated into lacustrine sediments. Piedade *et al.* (1992) estimated that *E. polystachya* is an important source of carbon retention in the Amazon region.

Armentano (1980) showed that draining of wetlands, especially for agriculture, turns them into a considerable source of carbon for the atmosphere. This author calculated that through drainage activities, $0.03 \times 10^9$ to $0.37 \times 10^9$ tons of carbon are liberated into the atmosphere per year. For the tropics, different types of alteration of natural wetland conditions lead to input of $0.07 \times 10^9$ to $0.18 \times 10^9$ tons of carbon per year (Lugo *et al.*, 1990). Filling of mangrove swamps also results in a large carbon input to the atmosphere, $0.07 \times 10^9$ tons/year (Armentano, 1980). It should be emphasized that the carbon liberated from wetlands represents, in large part, the carbon fixed by the primary producers of these environments. With liberation of the carbon fixed by photosynthesis, mainly by oxidation, wetland productivity is reduced, which in many cases represents a reduction in fish production.

For Amazonian wetlands, mainly represented by the river-floodplain system, Junk (1985) showed that with their transformation into pastures dominated by *Cynodon dactylon*, carbon losses are counterbalanced by the fixation rates of primary producers. However, these areas come to function as net carbon exporters, as the original vegetation is burned and organic carbon is exported to the atmosphere and then to local bodies of water, in dissolved and particulate form.

## Types of Wetlands in Brazil

Brazil has both continental and coastal wetlands. Continental wetlands especially are known by many names, some of which vary in different parts of the country. Local terms for wetlands and some approximate English equivalents include: *banhado*, *brejo*, and *pântano* (all meaning marsh, swamp, or bog), *pantanal* (extensive swampland, particularly the Pantanal of Mato Grosso), *igapó* (periodically inundated riverine wetland), *várzea* (bottomland along a watercourse), *campo úmido* (hillside flush marsh), *lameiro* (slough, quagmire) and *pampas* (grasslands), among others. Brazil's continental wetlands fall into four subgroups: 1) wetlands formed by river-floodplain systems (várzea, igapó, pantanal, *etc.*); 2) wetland associated with ponds and lakes (*brejo*, littoral zone, *etc.*); 3) wetlands in areas of high groundwater levels and/or accumulation of stream waters (*brejo*, *pântano*, *campo úmido*, *lameiro*, *etc.*); and 4) artificial wetlands formed mainly by construction of reservoirs and damming of rivers and streams for highways. Coastal wetlands are of five subtypes: 1) mangroves; 2) estuarine wetlands; 3) beach wetlands; 4) salt marshes; and 5) wetlands associated with lagoons.

### *Wetlands of River-Floodplain Systems*

The river-floodplain system consists of a complex of ecosystems including rivers, marshes, channels, lakes, islands, and transition zones. The latter were termed

"Aquatic-Terrestrial Transition Zone" (ATTZ) by Junk *et al.* (1989). These ecosystems interlink, notably during the flood phase, becoming more or less individualized when the waters recede. The river-floodplain system has as one of its main characteristics a high degree of geomorphological dynamism, determined by erosion and sedimentation processes. As a consequence of these processes, the landscape is constantly modified, which directly interferes with the processes of ecological succession.

Another characteristic of the river-floodplain system is the alternating periods of flooding and receding waters, which results in great variations in water level. This alternation imparts very special characteristics, such as the transformation of habitats, for example: lentic to lotic to lentic, and terrestrial to aquatic to terrestrial. Floodplain habitats can be profoundly altered, becoming differentiated during the low water phase, and more similar to each other during high water (Thomaz *et al.*, 1997).

In Brazil, the greatest extent of wetlands is found in river-floodplain systems, including some of the largest systems of their kind in the world. Among these are the floodplain of the Amazon River and its tributaries, covering approximately 300,000 $km^2$ (the literature is contradictory as to the exact extent of this floodplain); the Paraná River (250,000 $km^2$; Agostinho & Zalewski, 1996), and the Paraguay River (the Pantanal of Mato Grosso, 250,000 $km^2$; Tundisi, 1994). No less important is the extent of the river-floodplain system of the small tributaries of the Amazon, which according to Tundisi (1994) covers about 1,000,000 $km^2$ within the Brazilian territory.

The variation in water levels as a predominant factor in determining the ecological characteristics of the river-floodplain systems was noted by early European travelers throughout Amazonia. An example is the references made by the Portuguese Commander Pedro Teixeira, who explored the Amazon River in 1637. In his diary, Commander Teixeira mentioned the importance of floods for *várzea* fertility (Porro, 1992). More recently, several investigators have discussed the variation in water levels of the river-floodplain system according to an ecological perspective (*e.g.* Junk *et al.*, 1989). For these authors, the variation in water levels represents the chief forcing factor in these systems. The influence of this phenomenon on community dynamics and ecological processes in these systems can be compared to the influence of variations in temperature and photoperiod ón temperate ecosystems.

Variation in water levels in river-floodplain systems should be viewed as a regime of pulses, consisting of two distinct phases: flood and low water (Fig. 1). This pulsing system has been called by different names, such as flood pulse (Junk *et al.*, 1989), hydrological pulse (Neiff, 1990), among others. Neiff's (1990) terminology is considered more appropriate, since it describes the complete cycle.

Indeed, the hydrological pulse is a temporally continuous system, with the high water phase as one extreme, and low water at the end of the receding water phase as the other. To help in understanding the principal phases of the hydrological cycle, some investigators such as Bozelli & Esteves (1991) and Esteves *et al.* (1994) employed the following terms: flooding, high water, receding water (drawdown), and low water phases. The concept of temporal continuity between flooding and receding waters is mainly applicable to large floodplains such as the Amazon River. In this type of river-floodplain system there is perfect symmetry between the phases, each lasting six months. These systems obey an unimodal flooding pattern. In floodplain systems associated with smaller or lower-order (tributary) rivers, the hydrological pulse may be of shorter duration, generally only a few days, and multimodal with few to many annual flood events. An example of this type is the Mogi-Guaçu River and its floodplain in the state of São Paulo. The plant and animal species of the latter environments are adapted to the local flood phenomena. Even large rivers such as the Paraná may have up to three flood pulses, each lasting up to three months, in a single seasonal cycle (Cardigan & Neiff, 1992; Thomaz *et al.*, 1997).

*Influence of the Hydrological Pulse on the Abiotic Environment*

Large temporal changes in the abiotic characteristics of river-floodplain systems induce selective patterns which lead to the establishment of characteristic animal and, above all, plant communities. These characteristics can be seen in the many adaptations to the different peculiarities of the various ecosystems found in the river-floodplain system. This was one of the main reasons that so many limnologists and terrestrial ecologists have had difficulty in applying classical ecological concepts to river-floodplain systems. In order to understand these systems, the lotic ecosystems (principal rivers and their smaller tributaries), the lentic systems (*várzea* lakes, oxbow lakes), and the transition region (ATTZ) must be considered independently.

Among the three principal types of ecosystems in river-floodplain systems, lakes have been well studied as regards abiotic variables. In these ecosystems, patterns of nutrient cycling have received special attention and are indicated as one of the main factors responsible for the high productivity of the lakes (Schmidt, 1973; Roland, 1995; Rai & Hill, 1984; Paes da Silva & Thomaz, 1997).

The many investigations carried out in Brazilian river-floodplain systems have demonstrated that river flooding has an enormous influence on the ecosystems (Junk, 1985; Melack & Fischer, 1990; Neiff, 1990; Thomaz *et al.*, 1992). One of the most evident consequences is the establishment of anaerobic conditions in the inundated soils (Camargo & Esteves, 1995). Studies on the Trombetas River floodplain have shown that following flooding of *igapó* forest soils rich in organic matter in different stages of decomposition, the water of the lakes becomes hypoxic or anoxic (Barbieri, 1995). In such conditions, according to Knowles (1982), reducing conditions predominate in the flooded soils and in the water, resulting in the formation of toxic gases such as methane and sulphide. During the flood phase, the water of Amazonian *várzea* and *igapó* forests may rise several meters. These newly formed aquatic environments are characterized by low oxygen concentrations, especially in the lower part of the water column, and by high concentrations of dissolved carbon, particulates, and nutrients such as phosphate, nitrate, and ammonia (Barbieri, 1995). Water quality in the floodplain lakes is also strongly influenced by the flooding. In this manner, during the flood stage and with the increase in depth of the water column, thermal stratification occurs, forming layers that may differ chemically and biologically. The formation of an anoxic hypolimnion with higher concentrations of phosphate and ammonia is a characteristic of these lakes during the flood phase.

Table 2 presents values for some environmental variables in Lagoa do Mato, an oxbow lake on the Mogi-Guaçu River floodplain. According to Camargo & Esteves (1995), flooding of Lagoa do Mato by water from the Mogi-Guaçu, which occurs between November and January, is of major importance for its enrichment. At this time, part of the shoreline vegetation, especially the plants not adapted to flooding, dies with subsequent release of nutrients. Additionally, water turbulence resuspends sediments and nutrients in the water column. On the other hand, during the receding water phase, mixing of the water column reaches its maximum and the deeper layers become oxygenated. At this time there is frequent nutrient input into the euphotic zone.

Table 2. Environmental variables in Lagoa do Mato, an oxbow lake on the Mogi-Guaçu River floodplain, State of São Paulo, in 1987. (Camargo & Esteves, 1995).

| Environmental Variable | Drawdown | Filling |
|---|---|---|
| Transparency (m) | 1.2 | 0.3 |
| Temperature(°C) | 19.5 | 25.0 |
| pH | 6.0 | 6.4 |
| Electric Conductance. (µs/cm) | 15.0 | 50.0 |
| Dissolved Oxygen (mg/l) | 6.0 | 2.5 |
| Orthophosphate (µg/l) | 5.0 | 14.0 |
| Total Phosphate (µg/l) | 7.5 | 60.0 |
| N- Ammonia (µg/l) | 5.0 | 48.0 |
| Nitrate (µg/l) | 10.0 | 175.0 |
| Total Nitrogen (mg/l) | 0.8 | 12.0 |
| Reactive Silicate (mg/l) | 0.1 | 3.0 |

Stratification and destratification of the water column in floodplain lakes, especially during the flood phase, may occur daily (Macintyre & Melack, 1984; Lansac-Tôha *et al.*, 1995). In order for stratification and destratification to occur, appropriate weather conditions must be present, such as atmospheric cooling for a sufficient period to promote cooling of the epilimnion, and even the presence of weak winds. Daily stratification and destratification may also be responsible for nutrient input into the water column through resuspension of sediments (Junk, 1984; Tundisi *et al.*, 1984; Pagioro *et al.*, 1994). Thus, daily nutrient pulses observed in floodplain lakes together with seasonal pulses (rising *vs.* receding waters) represent the principal nutrient input that maintains the high phytoplankton primary production of these ecosystems (Paes da Silva & Thomaz, 1997).

### *Influence of the Hydrological Pulse on Plant Communities*

The organisms inhabiting river-floodplain ecosystems are more or less adapted to the extreme variation in ecological conditions that characterize these environments. The organisms of the transition zones (ATTZ) show the most extreme adaptations, resulting mainly from selection pressures imposed by the great degree of variation in the ecological characteristics of these environments.

According to Junk *et al.* (1989), the predictable and prolonged rising and receding waters of large rivers favor the development of anatomical, morphological, physiological, and frequently behavioral adaptations of aquatic and terrestrial organisms inhabiting river-floodplain ecosystems.

In lakes of river-floodplain systems, the changes observed in community structures during a hydrological pulse are considerable. These changes are especially notable in the primary producers. In Amazonian floodplain lakes, regardless of water type (black, clear, or white), sharp alterations in the phytoplankton community structure are observed, reflected in the values of primary production (Schmidt, 1973).

Investigations by Huszar (1994) in Lago Batata on the floodplain of the Trombetas River showed that the hydrological pulse was the main agent affecting seasonal succession of the phytoplankton community. The flood event abruptly interrupts the stage of greatest community organization, returning it to the initial stages, with broad changes in community structure. Huszar (1995) suggested that this phenomenon is reminiscent of spring circulation in temperate lakes.

During the receding water period, the relative hydrological stability favors intense community development, with increasingly complex successional stages. This is demonstrated by carbon concentration and species richness and diversity of the phytoplankton (Tables 3 and 4; Huszar, 1994). In the great majority of Amazonian floodplain lakes investigated up to now, the highest values for phytoplankton primary production were obtained during receding waters, and the lowest during flood stage (Schmidt, 1973; Roland, 1995). In Lago Batata, a value of 620 mg C/m$^3$/day was measured during the 1991 receding water phase, while during the flood stage of the same year, a more than fourfold lower value of 120 mgC/m$^3$/day was recorded.

Table 3. Principal phytoplanktonic organisms in Lago Batata (State of Pará) during the low water and flood stages of 1989 (Huszar, 1994).

| Drawdown | Filling |
|---|---|
| *Lyngbya cenense* | *Eucapsis alpina* |
| *Oscillatoria limnetica* | *Synechocystis aquatilis* |
| *Oscillatoria geminata* | *Chlorella homosphaera* |
| *Chlorella homosphaera* | *Cryptomonas marsonii* |
| *Mougeotia aff. delicata* | |
| *Cryptomonas aff. marsonii* | |

Table 4. Characteristics of Lago Batata (State of Pará) during the low water and flood stages of 1989 (Huszar, 1994).

| Variable/Attribute | Drawdown | Filling |
|---|---|---|
| Area ($Km^2$) | 18 | 31 |
| Depth of Sampling Site (m) | 1.8 | 9.0 |
| Phytoplanktonic Carbon (mg/l) | 0.81 | 0.01 |
| Species Richness (Number of Taxons) | 28 | 0.5 |
| Species Diversity (Bits/Individual) | 4.01 | 1.77 |

Another important aspect is the year-to-year variation in phytoplankton production. Roland (1995) compared phytoplankton production over a three-year period (1989-1991), finding the highest values during the first year. During that year (1989), the Trombetas River rose to one of the highest flood levels ever recorded (48.51 m), while water levels in the following years rose no higher than 46.52 m. These results indicate the strong relationship between levels of phytoplankton primary productivity and the hydrological pulse.

In Amazonia, water type (clear, white or black) is an additional factor in the structure of the aquatic macrophyte community. In white-water environments, because of greater nutrient availability, the aquatic macrophyte communities have higher species diversity than the communities of clear and black waters (Junk & Howard-Williams, 1977). Investigations of the biomass and productivity of some species of floodplain aquatic macrophytes have shown that the highest values occur during the rising water phase (Junk & Piedade, 1993).

Junk & Piedade (1993) reported 388 species of non-epiphytic herbaceous plants in lakes in the area of Manaus alone. Of these, four species have been intensively investigated: *Paspalum fasciculatum*, *Paspalum repens*, *Oryza glumaepatula* (= *Oryza perennis*), and *Echinochloa polystachya*. *Echinochloa polystachya*, a $C_4$ plant (highest efficiency of solar energy conversion) shows extremely high values of biomass production compared to other Amazonian floodplain species (Piedade *et al.*, 1991). According to these authors, the fact that this species maintains a considerable part of its vegetative structure out of the water further maximizes biomass production. These characteristics enable *E. polystachya* to attain one of the highest values of primary production yet recorded for plant communities: 108 tons/hectare/year. Moreover, this value is reached in only six months. In his classical review of primary production in aquatic macrophytes, Westlake (1963) reported values for aquatic macrophytes between 8 and 60 tons/hectare/year. Lieth & Whittaker (1975) estimated the corresponding value for tropical forest productivity at 25 tons/hectare/year.

Table 5 shows values of primary production of *E. polystachya* compared to other tropical aquatic macrophytes. This species, together with *Cyperus papyrus*, attained the highest values of biomass and productivity. In *C. papyrus* much of the biomass is in the rhizomes and is the result of several periods of production. The same does not occur with *E. polystachya*, in which the rhizome biomass is negligible (Piedade *et al.*, 1992). The high productivity of *E. polystachya* is even more remarkable considering the ecologically unfavorable conditions of floodplains, *i.e.* their ecological instability, changing from aquatic to terrestrial environments in the space of a few months.

Table 5. Biomass and productivity (dry weight) of some tropical macrophytes (Piedade *et al.*, 1992).

| Species | Maximum Biomass (Ton./ha) | Annual Productivity (Ton./ha) | Regions |
|---|---|---|---|
| *Oryza glumeapatula* | 40 | 40 | Australia |
| *Eichhornia crassipes* | 15 | 15-40 | USA |
| *Cyperus papyrus* | — | 48-143 | Africa |
| *Paspalum fasciculatum* | 28 | 39 | Brazil |
| *Saccharum officinarum* | 73-85 | 108 | Indonesia |
| *Echinochloa polystachya* | 70 | 108 | Brazil |

Many species of aquatic macrophytes such as *E. polystachya* that inhabit floodplains are r-strategists, according to the definition of Pianka (1970). These are species with rapid growth, precocious maturation, and characteristic reproduction (via seeds or vegetative reproduction). In ecologically very unstable habitats such as floodplain systems, rich in r-strategist species, interspecific competition must be intense. However, Junk & Piedade (1993) found no such competition in the Amazon *várzea* forest. They attributed to the hydrological pulse the capacity to return annually to the initial seral stages of succession, seen by Odum (1983) as intermediate between ecosystem youth and maturity. The production of flood-resistant seeds is an additional characteristic of these species (Junk & Piedade, 1993). The existence of the r-strategist floodplain species is directly associated with two highly important factors, as indicated by Piedade *et al.* (1992): high nutrient concentrations in the sediments, and an efficient system of photosynthesis.

*Oryza glumaepatula*, known regionally as "*arroz bravo*" or wild rice, is another very common Amazonian aquatic macrophyte contributing significantly to biomass production. Studies by Junk & Piedade (1993), Rubim (1995) and Enrich-Prast & Esteves (unpubl. data) showed that the highest biomass values for this species are reached during the rising water phase. Rubim (1995), in floodplain lakes of the Rio Negro, a tributary of the Amazon, demonstrated the close relationship between biomass production by *O. glumaepatula* and the hydrological pulse. During the dry phase (October-December), there is prolific germination of seeds deposited in the sediment during the previous flood. Following germination, growth is slow and the plants reach a mean height of 15 cm in 50 days, or 0.32 cm/day. With the beginning of the rains and even more during the flood stage, *O. glumaepatula* plants grow rapidly, reaching maximum size during highest water levels (approximately June-July). During this period, the daily growth rate may reach 7.0 cm and the biomass 1,300 g dry weight/m$^2$.

*Paspalum fasciculatum* is a typical herbaceous plant, widely distributed on Brazilian floodplains, especially in Amazonia. This species reaches its highest biomass during the receding water phase, when the sediments are exposed. According to Junk & Piedade (1993), biomass values increase as a function of the duration of the receding water phase, *i.e.* the longer the plants are not flooded, the higher the biomass. In a 220-230 day growing season (unflooded), Junk & Piedade (1993) obtained values for this species of 53.6-57.6 tons/hectare.

A common characteristic of the tree species of floodplain systems is adaptation to the unfavorable ecological conditions imposed by this environment (see reviews by Lobo & Joly; Pimenta *et al.*; and Scarano in this volume). One of these is the anaerobic conditions which occur with flooding in the lower part of the water column and especially in the "soil". Another common factor is the formation of sulphide gas in flooded sediments, which is quite toxic to the roots (Ridge, 1987). Anatomical adaptations of the vegetation to overcome scarcity of oxygen are less frequent than are physiological adaptations. The presence of aerenchyma associated with lenticels is an adaptation not often found, except in the case of the palm *Mauritia flexuosa*, which develops this feature when its root system is flooded (Worbes, 1989).

Changeover from aerobic to anaerobic metabolism is the most frequent adaptation of herbaceous vegetation to flood conditions. In species utilizing this adaptive strategy, metabolism (ATP production) is also reduced, malate is accumulated and excreted, and in some cases, toxic products such as ethanol are also formed (Crawford, 1982). The excretion of these compounds is an extremely important adaptive strategy, since they can cause acidosis and lead to cell death (Mitsch & Gosselink, 1993).

Data on the respiratory metabolism of tree species in Brazilian floodplain systems are very sparse. Junk & Piedade (1993a) observed that *Salix humboldtiana* and *Macrolobium acaciaefolium* meet energy demands anaerobically, producing and accumulating malate and ethanol that are metabolized at the beginning of the dry season. Junk & Piedade (1993b) noted that some species, such as the small palm *Astrocaryum jauari*, may respire aerobically and anaerobically simultaneously when their root systems are submerged. In these species, the aerenchyma tissue occurs in the roots, which carry out aerobic respiration.

Another factor worth of mention is the high frequency of species that accumulate large quantities of starch in their roots, which is utilized in respiration during submersion (Setter *et al.*, 1987). Herbaceous plants of Amazonian floodplains form cambial growth rings when flooding interrupts cambial activity (Worbes, 1989). According to Junk (1989), the rings are formed annually as a result of flooding. The age of an individual can therefore be determined from the number of growth rings. In temperate zone trees, growth rings are formed during winter, that is by the reduction of metabolism at cold temperatures. Another notable characteristic of trees, and frequently of herbaceous plants on floodplains, is the pattern of seed dispersal by water (hydrochory), by animals (zoochory), or a combination of these processes. Several investigators (e.g., Goulding, 1980) have demonstrated the great importance of fish in seed dispersal. The tambaqui (*Colosoma macropomum*), a commercially valuable fish species, feeds basically on the fruits of trees of the ATTZ. Seed dispersal via water occurs mainly in the deeper parts of the water column since most seeds are very dense and sink easily. On the other hand, some species (e.g., *Vatairea guianensis*, *Aldina latifolia*, and *Macrolobium acaciaefolium*) produce light or winged fruits that float (Barbieri, 1995).

In conclusion, the great diversity of species and wide variety of adaptations found in the vegetation of Brazilian river-floodplain wetlands may result mainly from the following: 1) the absence of major changes in climate since wetland formation, and the characteristic tropical climate; 2) the possibility of predictable flood and dry periods, which favor the appearance of adaptations; 3) the fluvial dynamics, which favor continuous formation of new habitats, which may be settled by many species; and 4) the fertility of the soils and sediments, in large part a result of the fluvial dynamics (hydrological pulse).

## Artificial Wetlands

The construction of artificial wetlands in Brazil dates back to imperial times, when the first reservoirs, called "*açudes*" were built in the Northeast, especially in Ceará. The *açudes* were intended mainly for water storage and fish farming. As demand for electrical power increased in the second half of the present century, many reservoirs of different sizes were constructed, initially in the southeastern part of the country. More recently in Central, Northeastern, and Amazonian Brazil, reservoirs have been built, mainly for electrical power production, that cover many square kilometers, such as the 2,300 $km^2$ Balbina Reservoir in the state of Amazonas (Tundisi, 1994).

The transformation of a lotic environment (river) into a lentic environment (reservoir) brings about complex changes in community succession and in patterns of nutrient cycling, besides having enormous social and political consequences. Poorly understood consequences of these activities in Brazil are the concomitant disappearance of typical river-floodplain wetlands and the formation of new types of wetlands from damming of rivers. The extent of the wetlands thus formed is due primarily to the morphometry of the reservoir. In Brazil, most reservoirs are dendritic, with several more or less isolated compartments. These characteristics make possible the formation of extensive artificial wetlands.

The new wetlands are usually formed in forested areas, especially in Amazonia, and in often fertile agricultural lands, as in the South and Southeast. The wetlands are initially colonized by aquatic macrophytes, generally emergent species such as *Typha domingensis* and several species of Gramineae and the genera *Eleocharis* and *Pontederia*, among others. In this phase, floating macrophytes such as *Salvinia* sp., *Eichhornia crassipes* and *Pistia* sp., the populations of which are constantly being replaced, are also common. When conditions of water turbidity become more favorable, the new wetlands can be colonized by submerged macrophytes such as *Utricularia* sp., *Mayaca fluviatilis*, *Myriophyllum brasiliensis*, *etc*.

Ecological conditions favorable to photosynthesis, such as light, nutrients, and the absence of predators in these new habitats, make it possible for the aquatic macrophytes to produce large quantities of biomass. The biomass produced is responsible for the growth of complex food webs, in which fish and birds are the main top consumers. These habitats are thus of great importance since they favor the reproduction of these organisms.

In some cases, conditions favorable to growth, production of biomass, and reproduction (especially reproduction of plants) have caused these plants to become "weeds", as they are considered by many technicians working in reservoirs. Numerous cases of this phenomenon are found in Brazil including several Amazon reservoirs in which extensive areas were covered by emergent aquatic macrophytes such as *Scirpus cubensis*, *Eichhornia crassipes*, *Pistia* sp., and *Salvinia* sp. In Sobradinho Reservoir in the state of Pernambuco, growth of the emergent macrophyte *Egeria* sp. has reached alarming levels, compromising the main energy-producing function of the reservoir. According to Grillo (pers. comm.), the extraordinary growth of this species resulted from enrichment of reservoir water by the tributaries draining surrounding fertilized areas. The Sobradinho region of the São Francisco River valley is one of the most productive regions for raising fruits and vegetables for export in Brazil.

The hydrological cycle and the mode of operation of water release from a reservoir are the main factors responsible for structural and functional transformations of wetlands associated with reservoirs. Another characteristic of wetlands associated with reservoirs is the great variation in area. This is a consequence of variation of the hydrological cycle and, more importantly, of the operation of the reservoir. Because of these factors, the water level of a reservoir may rise, flooding new areas. The areas occupied by macrophytes may also increase, and so may the loss of the unadapted terrestrial vegetation. Conversely, when water levels fall, extensive areas are exposed and the following phenomena occur:

1) The death of aquatic macrophytes, making a large amount of biomass available to the detritus food chain and generating a considerable load of nitrogen and phosphate for the next flood period. This phenomenon was observed in the Lobo Reservoir in the state of São Paulo (Esteves & Thomaz, 1990) and Samuel Reservoir in Roraima, which was reduced from 600 to 200 $km^2$ (Tundisi, 1994).

2) If the exposure is sufficiently prolonged (several months), the exposed areas are colonized by many terrestrial, especially herbaceous plants. Their rapid germination and growth is facilitated by the large quantities of nutrients in the soils of exposed wetlands. During the next flood this vegetation dies and the biomass, in the form of detritus, becomes important for fish production. The existence of this process makes investigations of Brazilian reservoirs urgently necessary, as its understanding will permit sound ecological ecosystem management, particularly to enhance productivity.

As discussed previously, varying the water level, *i.e.* maintaining the hydrological pulse, is clearly and fundamentally important in maintaining the productivity of some reservoirs, especially those formed by rivers in nutrient-poor drainage basins. The availability of basic limnological data to reservoir administrators can serve as an excellent basis for sound management of these ecosystems.

Floodplains associated with reservoirs may also cause problems in their functioning, especially in reservoirs used for energy production. The most frequent problem is the increase in aquatic macrophyte populations in the surrounding wetlands. Large stands of macrophytes of many square meters in area may break loose and move into the central part of the reservoir and thence into the area of the turbines. The plants may reduce water flow to the turbines and interrupt operations.

Accumulation of aquatic macrophytes may cause problems with fishing and recreation, as well as accelerating the process of sedimentation in the reservoir, caused by large biomass production when a portion is not totally decomposed and accumulates in the environment.

## Man's Impact on Wetlands

In Brazil, wetlands have had their natural states altered or have been destroyed altogether by reservoir construction, dredging, draining, and filling. Although hundreds of reservoirs have already been constructed in Brazil, few data are available on the effect of these projects on wetlands. Damming a river affects not only the wetlands associated with its main channel, but also the areas downstream from the dam and its affluents in the area influenced by the new body of water.

According to Agostinho *et al.* (1995), in the Upper Paraná River alone there are 130 reservoirs with dams over 10 meters high, 26 of these over 100 $km^2$ in area. The impact of these reservoirs on the hydrological regime, according to these authors, is to raise the minimum mean low water levels, and lower the maximum mean high water levels. Changes in the hydrological pulse must also be considered, which are then controlled, not by the natural hydrological regime, but by the operation of the dams. Flooding may therefore occur weekly or even daily rather than seasonally, as happens in the Upper Paraná during the period of low water (Thomaz *et al.*, 1997).

As a result of dam construction and drainage control, fish populations are affected by having their natural migration limited, and by increased mortality of juvenile stages in the floodplain lakes (Agostinho & Zalewski, 1996). In the area affected by a reservoir, a large part of the flooded vegetation will die and those areas will be recolonized by aquatic macrophytes. Considerable changes may thus occur in the food chains webs of the affected areas. Downstream from the dam, because of attenuation and altered frequency of the hydrological pulse, many changes may occur including changes in the pattern of seed dispersal linked to the hydrological pulse, and increased plant mortality. Moreover, intense sedimentation in the reservoirs often reduces the load of suspended matter and nutrients downstream. There is some evidence that the phosphorus load in the Paraná River, for example, was reduced following the construction of large dams in its basin (Pedrozo & Barreto, 1988; Agostinho *et al.*, 1995).

Dredging in wetlands is mainly aimed at extracting resources such as sand (very frequent in rivers and lakes of the state of Rio de Janeiro), lime (especially common in coastal lakes and lagoons), and gold (common in northern Brazil). Besides increasing water turbidity, dredging inevitably destroys habitats, especially the benthos. In several parts of Brazil in the 1960s, wetlands were intensively drained and often filled. The chief motive for this activity was elimination of the habitats of disease-transmitting mosquitoes, particularly yellow fever vectors.

The use of wetlands for raising animals has become common practice throughout Brazil. The effect of this practice on the ecosystems is as yet very poorly understood. In several parts of the country, wetlands are especially exploited during low water, when ranchers move their cattle herds to these areas. The intense growth of terrestrial plants makes excellent grazing during the dry season, when the regular pastures are in many cases unable to support the herds. Over time, trampling by the animals compacts the soil and sediments, impeding growth of aquatic vegetation during the flood phase. Rarely, the ranchers cut down wetland trees, with the idea of favoring growth of herbaceous plants (Agostinho & Zalewski, 1996). Additionally, during the dry season extensive areas may be burned to promote plant growth.

Total or partial substitution of cattle herds by the Asian buffalo has considerably impacted several regions of Brazil. In contrast to cattle which are removed from wetlands in flood season, buffalo remain there during the entire hydrological cycle. The herbaceous vegetation is trampled during low water, and the aquatic vegetation is trampled during flooding. This has led to serious reduction in fish production in some regions. In wetlands in the region of Pinheiro Viana and the *várzea* of the Pericumã River, state of Maranhão, fish production has been drastically affected. Data from fishermen on the Pericumã indicate that in 1988 it was possible to harvest about 5,500 kg/day. In 1995, about ten years after the introduction of buffalo, the harvest was reduced by more than half. In the affected areas of Maranhão state there have already been conflicts resulting in deaths, between buffalo ranchers and fishermen.

The use of wetlands is a very ancient practice in Brazil. Reports by Friar Carvajal, chronicler of the pioneer expedition of Francisco Orellana along the Amazon in 1541 and 1542, indicate that the *várzeas* were already utilized for planting manioc (Porro, 1992). At that time, just as today, the largest human concentrations in Amazonia were in the region's wetlands (Ayres, 1995).

At present, many plant species, most commonly rice, are cultivated in Brazilian wetlands. Wetlands are being filled in, for different reasons, throughout Brazil. The reasons include increased land area for urban or rural properties, highway construction, and mining.

## Acknowledgements

I thank my students for their support and to the various colleagues who revised this text. I also thank Pronex/Finep for funding.

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