Amazonian floodplains : their ecology, present and potential use

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SUMMARY

Wetland ecosystems of the Amazon basin belong mostly to the flood-plain-type. An analysis of the ecological parameters acting in flood-plains shows that they differ in many ways from other wetland types. The large annual water level fluctuations cause a periodic shift between aquatic and terrestrial phases, which influence the abiotic and biotic events in a decisive manner. Many morphological, physiological and ethological adaptations to these special conditions are exhibited by the local organisms.

The nutrient cycle is strongly influenced by the river. However internal cycles and a large transfer of nutrients between the aquatic and terrestrial phases, due principally to aquatic and terrestrial herbaceous plants, require special attention. Floodpains may therefore be designated as intermediate systems between rivers (open systems) and lakes (closed systems). Land and water phases have to be considered as a single unit in describing the nutrient cycles. The overwhelming effect of the water level fluctuation prevents maturation of the ecosystem, maintaining it permanently at an immature stage. Depending on the concentrations of mineral nutrients of the connected rivers, the floodplains show high natural production and decomposition rates, and great energy and nutrient exchange with the river.

In Amazonia, the nutrient-rich floodplains of white-water rivers (várzea), have a particularly great potential for agriculture and animal husbandry, if methods adapted to the occurrence of flooding are used. Any large-scale flood protection efforts will modify the system, reducing its high natural productivity. Increasing utilization of the varzeá by agriculture is expected to have an effect on the fish-stocks. In view of the great importance of inland fisheries as a protein source, intensive cooperation is needed between agronomists and fisheries biologists in the planning and realisation of floodplain projects, in addition to detailed studies of the effects of agriculture and animal husbandry on the fish-stocks, to avoid deleterious side-effects on the fisheries. Fisheries actually yields about 150 000 t of fish/year in the Brazilian part of the Amazon basin. This amount may be doubled if the highly selective fisheries is changed to better utilize under-exploited small species. In the light of the rapid growth of the human population, aquaculture must be developed to guarantee a long term supply of fish. Because of a lack of methods adapted to the high water level fluctuations, fish-farming seems to be difficult in the floodplains. Swampy areas beside small creeks offer better conditions, and permit protein production in areas which can be used neither for agriculture nor for animal husbandry.

KEY WORDS : Floodplains — Amazon — Ecology — Utilization.

RÉSUMÉ

LES PLAINES INONDÉES DE L'AMAZONIE : ÉCOLOGIE ET UTILISATION ACTUELLE ET POTENTIELLE

Les zones humides du bassin amazonien sont essentiellement des plaines inondées. Une analyse des facteurs écologiques associés aux plaines inondées, montre que ces milieux diffèrent par beaucoup d'aspects des autres types de zones humides. Les grandes variations du niveau de l'eau à l'échelle annuelle entraînent un passage périodique de la phase terrestre à la phase aquatique, et inversement, qui a des conséquences importantes sur le plan abiotique et biotique. Beaucoup d'organismes qui y vivent présentent en effet des adaptations morphologiques, physiologiques et ethologiques à ces conditions particulières.

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Le cycle des éléments nutritifs est fortement influencé par la rivière. Toutefois des cycles internes et un important transfert des éléments nutritifs entre les phases aquatiques et terrestres, dus surtout aux végétaux herbacés terrestres et aquatiques, nécessitent une attention particulière. Les plaines inondées peuvent par conséquent être considérées comme des systèmes intermédiaires entre les rivières (systèmes ouverts) et les lacs (systèmes fermés). Les phases aquatiques et terrestres doivent être considérées comme une seule unité pour décrire les cycles d'éléments nutritifs. L'effet de submersion par l'eau, en raison des fluctuations de niveau, empêche l'écosystème d'atteindre le stade de maturité et le maintient en permanence dans un stade immature. Selon les concentrations des éléments nutritifs dans les rivières auxquelles elles sont rattachées, les plaines d'inondation peuvent avoir une forte production et des taux de décomposition élevés, ainsi que des échanges importants d'énergie et d'éléments nutritifs avec la rivière.

En Amazonie, les plaines d'inondation riches en éléments nutritifs des rivières à eaux blanches (vàrzea) sont potentiellement intéressantes pour l'agriculture et l'élevage, si des méthodes appropriées prenant en compte l'inondation sont utilisées. Tous les efforts réalisés à grande échelle pour se protéger de l'inondation modifieront le système et réduiront sa productivité. L'utilisation croissante des « vàrzea » pour l'agriculture aura probablement un effet sur les stocks de poissons exploités. Considérant l'importance des pêches continentales en tant que sources de protéines, il est nécessaire que les projets visant à la mise en valeur des plaines inondées soient réalisés en coopération étroite par des agronomes et des biologistes des pêches. Des études détaillées sur les effets de l'agriculture et de l'élevage sur les stocks de poissons exploités sont également nécessaires pour éviter d'éventuels effets nuisibles sur les pêcheries.

Les pêcheries exploitent environ 150 000 tonnes de poissons par an dans la partie brésilienne de l'Amazonie. Cette quantité pourrait être doublée si les pêcheries, actuellement très sélectives, se diversifiaient et s'intéressaient également aux espèces de petite taille encore sous-exploitées.

En raison de l'accroissement rapide des populations humaines, l'aquaculture devrait être développée de manière à garantir l'approvisionnement en poissons à long terme. Mais le manque actuel de méthodes adaptées aux fluctuations du niveau de l'eau, ne permet pas d'envisager la pisciculture dans les plaines inondées. Les zones marécageuses proches des petits cours d'eaux présentent des conditions plus favorables permettant de produire des protéines dans des milieux qui ne peuvent être utilisés pour l'élevage ou l'agriculture.

MOTS-CLÉS : Plaines inondées — Amazonie— Écologie — Utilisation.

1. INTRODUCTION

Extending over 7 000 000 km² the Amazon basin represents the largest catchment area of a river system on earth with the largest area of tropical rain-forest (about 5 000 000 km²). In spite of its enormous dimensions and amazing biological diversity the region fell into almost complete oblivion for several decades after the crash of the rubber boom (caused by large scale planting of rubber trees *Hevea brasiliensis* in South-east Asia at the beginning of this century). However during the last 15 years the great industrial and agricultural development started by the Brazilian government has provoked a world-wide interest in the Amazon region and its future development. In this context, I should mention the announcement by the Brazilian government of the existence of enormous mineral resources, the intensive discussion between scientists, politicians and project managers about the potential of the Amazonian rain-forest for large-scale timber production, and the possibilities of using the region for agricultural purposes and cattle-raising. Agricultural development planning until now has concentrated on areas of Amazonia not subjected to flooding (so-called terra firme) covering more than 90 % of the area (ALVIM, 1973, 1978; SMITH, 1976, 1978; KLINGE *et al.*, 1981 and many others). Additionally, the terra firme seemed to be more suitable for the application of traditional agricultural methodology than the floodplains of the great rivers. However, the serious nutrient deficiency of the soil, which is characteristic of many areas of the terra firme in the Amazon basin, created problems for its utilization (GOODLAND and IRWIN, 1975; EDEN, 1979; SIOLI, 1980a, 1980b; COCHRANE and SANCHEZ, 1980, etc.). Detailed soil and vegetation maps, produced by the national aerial survey (RADAM), using aerial photography and remote sensing techniques, combined with ground-level surveys, led to a more realistic evaluation of the agricultural potential of the region. The maps reveal considerable geological variation within Amazonia and this has been taken into consideration in the recent evaluation.

The large floodplains of the Amazon river and some of its tributaries were shown to be areas of high agricultural potential. This evaluation agrees with the opinion of some ecologists and agriculturists who has already shown, some decades ago, that the floodplains of the Amazon and those of its tributaries rising in the Andes, have considerably higher levels of nutrients than the surrounding terra firme. They are thus especially appropriate for agricultural development, principally for annual crops and animal husbandry (Camargo, 1949, 1958; Sioli, 1950, 1956, 1957).

Based on these results the Brazilian government recently started an agricultural development programme for the várzea (PROVARZEA). Considering the population growth rate is about 3 % per year in Brazil, the development of agricultural activities in Amazonia is of great social importance and the utilization of the floodplains may contribute substantially to food production.

Is our knowledge of the ecology of floodplains in general, and the várzea of the Amazon in particular, sufficient to justify from the scientific point of view a large-scale agricultural development? If so, what recommendations should be made to permit optimal utilization of the area?

2. DISTRIBUTION, DEVELOPMENT AND ECOLOGICAL CLASSIFICATION OF THE AMAZONIAN FLOODPLAINS

The Amazon basin is characterized by the enormous river system of the Amazon and its tributaries. Lakes exist in the form of floodplain lakes and Ria-lakes. Shallow lakes, mostly supplied by rain water and sometimes temporary, exist in the savanna area of Roraima in the northern part of Amazonia.

The lack of deep-water lakes is a result of large-scale sedimentation processes which have prevented the development of lake basins. Central Amazonia represents the greatest tertiary sedimentation area on earth. Additionally, several authors suggest that tectonic movements of the archaic shields led to additional deposition of sediments about 2.000.000 years ago in Central Amazonia (Belterra formation) (Sombroek, 1966; Fittkau, 1974; Klammer, 1978).

Of decisive influence on the present aspect of rivers and landscape were the eustatic fluctuations of the sea-level during the last glacial period. About 25,000 years ago, the sea-level dropped to its minimum, about 100 m lower than today (Fairbridge, 1961). As a result of the increased gradient during this period Amazon and its tributaries cut large and deep valleys into the soft tertiary sediments of central Amazonia. Later the ensuing rise in sea-level dammed the rivers back in their own valleys. Because of the low altitude of central Amazonia (today 1 000 000 km² are less than 100 m above sea-level) the influence of this process extended to the slopes of the Andes in the west and to the slopes of the shields, of Guiana in the north, and that of Central Brazil in the South. The reduction of current speed induced sedimentation processes within the large river valleys. Rivers with a high sediment load like the Amazon have nearly filled up their valleys, forming a very complex floodplain with lakes, islands, river channels and levees, which are permanently being modified by further erosion and sedimentation. During periods of highest water level the entire floodplain is covered with water and the river occupies the whole glacial valley, in some places 50-100 km wide.

Rivers with low sediment loads, like the Rio Negro or Rio Tapajós, have not yet finished the infilling process of their valleys. The river mouth areas are very wide and deep and may, because of their low current speed, show a lake-like physical, thermal and biological stratification (Ria-lakes). The mouth area of the Rio Negro at Manaus is up to 12 km wide, and up to 100 m deep. However these dimensions are in conflict with the actual current speed of 0,81 m/sec. and a discharge of 66 800 m³/sec. measured by Oltman *et al.* (1964) soon after maximum flood.

Because of considerable differences in precipitation during the year in Amazonia, there are distinct rainy and dry seasons. Consequently, the water-level of the great rivers is subjected to yearly fluctuations, which reach an average of 10 m near Manaus (fig. 1), and on the lower Amazon about 4-6 m. Whereas during the period of low water large areas of the floodplains are dry land, these are completely inundated during extreme high water (fig. 2). The water-level of small rivers and creeks shows more irregular oscillations. During and after heavy rains, their small valleys are normally inundated for several hours or days but then dry up again. However the groundwater level in these valleys is always very high, and even during dry periods the ground is often water-logged.

The shallow lake basins in the savanna-area of Roraima are considered to be of aeolian origin (Reiss, 1973) having a characteristic circular shape. During the rainy season they are filled with rainwater, whereas during the dry season, they may dry up completely.

Swamps with large deposits of organic material (peat) occur in Amazonia only to a limited extent and under special hydrological conditions (Junk, *in press*).

The total area covered by floodplains in Amazonia is considerable. Unfortunately, there are no detailed data available. I estimate that the floodplains of the great rivers cover an area of about 120 000-150 000 km². There are no estimates for the total area of the shallow lakes of Roraima and the swampy areas, but the sum total of those swampy areas along the creeks in the whole Amazon basin may equal the total area of the floodplains of the great rivers, or even be several times larger.

3. HYDROCHEMICAL CLASSIFICATION

Sioli (1950, 1965) classifies Amazonian waters from a physico-chemical point of view into 3 types:

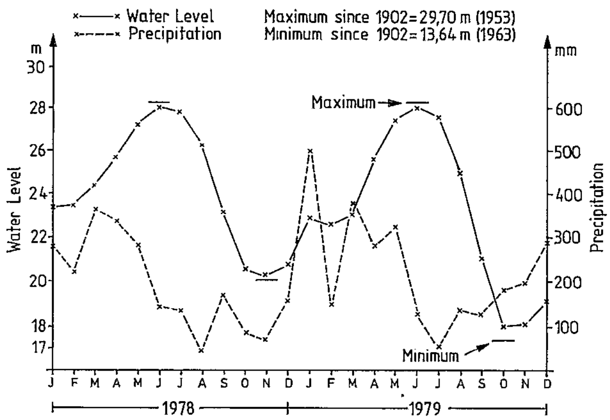
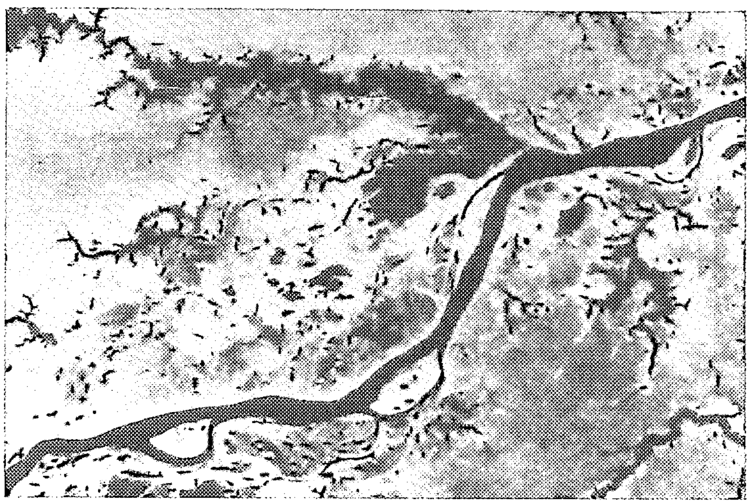


FIG. 1. — Water level fluctuations of the Amazon and precipitation near Manaus. (Water level data from Capitania dos Portos, Manaus; precipitation data from MARIA DE NAZARÉ GOES RIBEIRO, INPA, Manaus)



a

FIG. 2. — Aerial view of the várzea of the middle Amazon near Manaus during low water (09.12.76) (a) and high water (31.07.77)

b

(b) The photos do not show the extreme conditions that occur at times during these two periods because the difference in water level between the photos is only 8.62 m, while the mean difference is 10 m and extreme values reach 15 m. Furthermore, during high water, the dense inundation forest and aquatic macrophytes appear to be dry land, while, in fact, they conceal water beneath. The photos cover an area of about 90×50 km. (Photos by CNPq, INPE - Landsat - São Paulo) white-water, black-water and clear-water. White-water is relatively rich in nutrients and electrolytes, and pH neutral (pH 6,2-7,2). The catchment area of white-water rivers includes the Andean and pre-Andean area, and from these areas large quantities of fine inorganic sediments are transported by the rivers, giving the water a turbid greyish colour. Rivers like the Amazon, Purús or Juruá, have large floodplains because they have already filled their glacial valleys with sediments containing considerable quantities of clay minerals (illite, montmorillonite). The ion exchange capacity of such sediments is higher than that of the sandy and kaolinitic material forming the surrounding non-floodable areas (Irion, 1978). The floodplains are therefore more fertile than the surrounding non-floodable terra firme. Such floodplains of white-water rivers are called várzea. Black-water rivers are extremely poor in nutrients and electrolytes and of low pH (pH 3,8-4,9). Humic substances (humic and fulvic acids), originating from podzols and flooded forests cause a dark brownish to reddish coloration of the transparent water (Klinge, 1967, 1968; Paolini, 1979).

Clear-water rivers are transparent and greenish, but are, from a hydrochemical point of view, very heterogeneous. Depending upon the catchment area, the electrolyte concentration and pH values vary considerably. In general, the pH value is lower than in white-water (pH 4,5-7,8). The catchment areas of black-water and clear-water creeks lie in central Amazonia and in the shields of the Guyanas and Central Brazil. The sediment load is small because of the gentle relief of the catchment area and therefore, the great rivers of this type have not yet filled their glacial valleys. The sediment load is mostly of sandy material, however clear-water rivers in particular may become turbid during the rainy season when finer sediments are carried in the water. Floodplains of black-water and clear-water rivers are called igapó (Prance, 1979).

Recent detailed studies have confirmed the great hydrochemical variability of Amazonian waters, principally of the clear-water type (Gibbs, 1967, 1972; Furch and Junk, 1980; Stallard, 1980). In general, white-water may be considered as carbonate water with a high percentage of alkali-earth metals, whereas clear- and black-water may be considered as non-carbonate water with a high percentage of alkali metals (Furch, 1976, 1978; Furch and Klinge, 1978; Furch *et al.*, *in press*).

This somewhat simplified characterization of the hydrochemical situation of Amazonia must suffice for the explanation of the ecological problems discussed in the next sections. Additional studies are being carried out at present. More studies will be necessary in the future, in order to obtain sound background data for nutrient budget analysis of Amazonian waters and floodplains. For the present we may conclude that floodplains of black-water rivers are extremely poor in nutrients, those of the white-water rivers rich in nutrients, while those of the clear-water rivers may be considered of intermediate nutrient status.

4. ECOLOGICAL ASPECTS OF AMAZONIAN FLOODPLAINS

4.1. General considerations

The ecological situation of floodplains in general, and those of the Amazon and its tributaries in particular, is influenced fundamentally by alternation between aquatic and terrestrial phases. This change has fundamental consequences for most of the biotic and abiotic processes in the floodplains. Unfortunately little information exists about such areas and processes. Most of our knowledge refers either to the terrestrial or to the aquatic phase. Comprehensive studies covering both phases, are very rare. In our opinion this is due to the fact that floodplains fall between limnology and terrestrial ecology, and are therefore neglected by workers in both. Additionally, the scientific problems are very complex, demanding new concepts, an interdisciplinary approach and modified sampling techniques. Since, in many countries, principally in the industrialized world, the existing floodplains were long ago modified by man, scientists have since felt little need to study them in detail. Out of the 264 500 km² floodplain of the Danube for example, only some 5 000 km² are still liable to inundation. According to Welcomme (1979) it is eventually intended to reclaim the whole area, including the delta. The large floodplain of the river Rhine began to be modified in the middle of the last century, such that at present only very small areas are regularly flooded.

The major seasonal floodplains of the world are found in the tropics and sub-tropics. Increasing human pressure to utilize floodplains for fisheries, crop production and animal husbandry, as well as the impact of the construction of big dams, have led recently to more detailed studies on these areas, principally in Africa and South-East Asia. A general description of existing types of floodplains and their ecology in respect to fish and fisheries is given by Welcomme (1979).

Summarizing our existing knowledge, we may say that floodplains and their connected rivers or lakes represent a very complex habitat system. During peak flood, the area is inundated and becomes a predominantly aquatic system. As the water goes down the system becomes increasingly dry until the water level is at a minimum. During this period, the floodplain is a complex mosaic of terrestrial and aquatic habitats with many swampy transition areas. The dry areas may be covered with grasses. The savanna type of floodplain is characteristic for many African rivers. In Amazonia, only low lying areas and recently deposited sediments are covered with herbaceous plants. The floristic composition and density of the plant community depends on available moisture and nutrients. Higher parts are covered by floodplain forest, representing the final stage of plant succession. The pronounced terrestrial character of the Amazonian várzea is well documented by the fact that development of crop plantations requires additional irrigation.

Distributed over the floodplain are lakes of different origins e.g. ox-bow lakes, lateral levee lakes, lakes in abandoned channels, lakes in depressions formed by uneven aggregation of sediments during flood, swampy areas, etc. These aquatic habitats form refugia — or traps — for aquatic organisms during drought. They shrink considerably in size, or even dry out completely during dry periods. When the river level is rising, the whole area is flooded, again becoming an aquatic system. Only the highest levees may provide scattered islands of terrestrial habitats.

Welcomme (1979) stresses the point that floodplains form part of the functional river or lake system. There is no doubt about the close interaction between rivers or lakes and their associated floodplains with respect to the exchange of water, nutrients and the biota. However it would be unbalanced to consider floodplains simply as parts of the aquatic system. There are many relationships with areas outside the floodplains which, although less conspicuous are however very important, for instance with respect to species evolution (Erwin and Adis, 1982). The dynamics resulting from a large scale periodic variation of the land/water boundary, caused by the large fluctuations in water level has given floodplain systems a very specific character in comparison to other systems, both aquatic and terrestrial. Many of the morphological, anatomical, physiological and/or ethological adaptations of the colonizing organisms as well as differences in the nutrient and energy cycles, emphasize the distinctiveness of the system (Junk, 1980; Brinson *et al.*, 1981). The closest general similarity shown by floodplains, is to ecosystems influenced by tidal activities. However, the diurnal fluctuation between terrestrial and aquatic phases in tidal areas results in considerable ecological differences compared to floodplains subjected to annual changes between these phases.

For limnologists the special character of floodplains is evident whenever they try to apply limnological terminology concerning spatial parameters to floodplain lakes. Areas, which during high water must be considered as profundal, during medium water-level can be considered as littoral, and during low water become dry land. Thus there is a continuous change in the conditions in the biotopes creating difficulties in defining the terms 'aquatic' and 'terrestrial', and subsequently terms like 'allochthonous' and 'autochthonous', which are very important within the context of nutrient budget studies (Junk, 1980).

4.2. Adaptations of organisms under floodplain conditions

The organisms living in floodplains show a wide variety of adaptations to the change between the aquatic and the terrestrial phases. Purely aquatic plants and animals exist as well as purely terrestrial ones, and there are many of intermediate character. Therefore, for my purposes, given the ecological conditions of floodplains, it is better to use the terms 'aquatic' and 'terrestrial' in the sense of 'aquatic or with the main development period during the aquatic phase' and 'terrestrial or with the main development period in the terrestrial phase'.

Many plants and animals have developed survival strategies for unfavourable periods. Mobile organisms show both horizontal and vertical migrations. Vertical migrations between the ground and the canopy of the inundation forest are shown by many terrestrial invertebrates (Irmler, 1975, 1976, 1979; Adis, 1979). Large horizontal migrations are recorded for many fish species between the river proper and the floodplain (Lowe-McConnell, 1975; Welcomme, 1979; Goulding, 1979). Other survival strategies include resting stages, e.g. for terrestrial springtails (Beck, 1976), and for planktonic and perizoic crustaceans, sponges and mussels (Irmler, 1980). Many plants have also developed resting stages. Additionally, herbaceous plants show considerable morphological and physiological plasticity which enables them to survive the unfavourable period (Junk, *in press*).

In spite of these adaptations, losses in many of the populations are very high. Estimates from the Kafue river and floodplain system in Africa indicate differences in ichthyomass of 40 % between wet and dry seasons (University of Michigan *et al.*, 1971). Invertebrates and plant populations may have much higher losses, as shown by Beck (1976) for springtails and Junk (1970) for aquatic macrophytes. Many organisms compensate for these losses by high reproductive rates, often combined with short life cycles (r-strategy). Asexual, in addition to sexual reproduction is very common in many plants and invertebrates (IRMLER, 1981). Some species, however, have opted successfully for "K-strategy" as well, e.g. many fish species or some crabs. They ensure *high survival rates of juveniles* by a very *complex* system of parental care.

4.3. Production and decomposition

High reproductive rates and short life cycles result in a high production of organic material when the nutrient level in water and soil is adequate, as happens in the white-water floodplains. Phytoplankton production amounts to 6 t dry weight/ha/year, but is in part limited by reduced light penetration (SCHMIDT, 1973b). Herbaceous plants contribute significantly to net production. Standing-crop values of 30 t dry weight/ha in one vegetative period of 8 months are reported for some terrestrial and aquatic grasses (JUNK and HOWARD-WILLIAMS, *in press*). On the other hand, decomposition rates for these plants are also very high. HOWARD-WILLIAMS and JUNK (1976) report a 50 % loss of dry plant matter in litter bags, during the first two weeks of the aquatic period. Later on the rate of weight loss is reduced, and after 6 months about 15% of the initial weight still remains. Such rapid decomposition processes are a result of the permanently high temperature of about 30 °C and the relatively low cell-wall fraction of the herbaceous plants. Considering the high production rates, a considerable accumulation of organic material, and the formation of large peat deposits in Amazonia, could be expected, but normally this is not the case (NIKONOV and SLUKA, 1960). In this context, the regular change between aquatic and terrestrial phases is of decisive importance. During the dry phase good aeration of the soil permits rapid decomposition of the organic matter. This process is accelerated by terrestrial invertebrates which consume the organic detritus. If a dry phase is prevented by morphological pecularities of the lake basin, an accumulation of organic material occurs with concomitant oxygen deficiency and hydrogen sulphide development in the organic layers. An accumulation of organic material may occur in the form of floating islands or of deposits on the lake-bottom. Such organogenic landformation processes however do not occur on a large scale in the várzea, and do not develop beyond a certain stage because of the internal dynamics of the floodplain ecosystem (JUNK, *in press*).

4.4. Nutrient cycles and food webs

To a large extent the nutrient cycle is controlled by the intimate interrelationship between the Amazon river and its floodplain. During periods of rising water level nutrients are transported by the river into the floodplain where phytoplankton and macrophytes incorporate them into organic material. When the water retreats nutrients are transported back into the river, mostly as organic material, *influencing the food webs of the river itself, any delta* area and the adjacent marine environment. RITCHEY (1980, 1982) gives a value of 100 million tons of carbon per year transported by the Amazon to the sea. We may suppose that a considerable amount of this is derived from the floodplains.

Complex internal cycles of nutrients exist in the floodplains. Due to their enormous production capacity and biomass, terrestrial and aquatic herbaceous plants are particularly important. The role of macrophyte vegetation in swamps and in the littoral zone of lakes, with regard to general ecology, the nutrient budget and food chains has been stressed for both temperate and tropical regions (GAUDET, 1974; HOWARD-WILLIAMS and LENTON, 1975; HOWARD-WILLIAMS, 1977). Nutrient pumping from sediments to the water by macrophytes rooted in the ground is a well known phenomenon (KLOPATEK, 1978; PRENTKI *et al.*, 1978). In the floodplains macrophytes act in the aquatic phase as well as in the terrestrial one. This makes the evaluation of their activity and of the interactions with the whole system very difficult.

Our investigations in the várzea of the Amazon indicate that macrophytes retain some of the nutrients in the system, so enriching it to a certain extent. Nutrient transfer between aquatic and terrestrial phases principally by aquatic and terrestrial herbaceous plants seems to be particularly important. The nutrient transfer mechanism is based on the high capacity of aquatic macrophytes to concentrate nutrients, previously dissolved in the water, in their tissues. During periods of decreasing water level, many of these plants are deposited on the drying beaches. Terrestrial plants growing during this period have both the nutrients in the soil, and those of the decomposing aquatic plants at their disposal. When the water level is rising, the terrestrial plants decompose and release nutrients which then become available to the aquatic plants, in addition to the nutrients introduced into the system by inflowing river-water (fig. 3). Consequently, the system enriches itself until a new equilibrium is reached, and functions with a higher productivity than would be predicted from the nutrient levels of the river water. This internal nutrient cycle gives floodplain lakes a position intermediate between closed systems of lakes and open systems of rivers. The mutual exchange of nutrients between terrestrial and aquatic phases requires that a comprehensive analysis of the nutrient budget, including both the terrestrial and aquatic phases, is made.

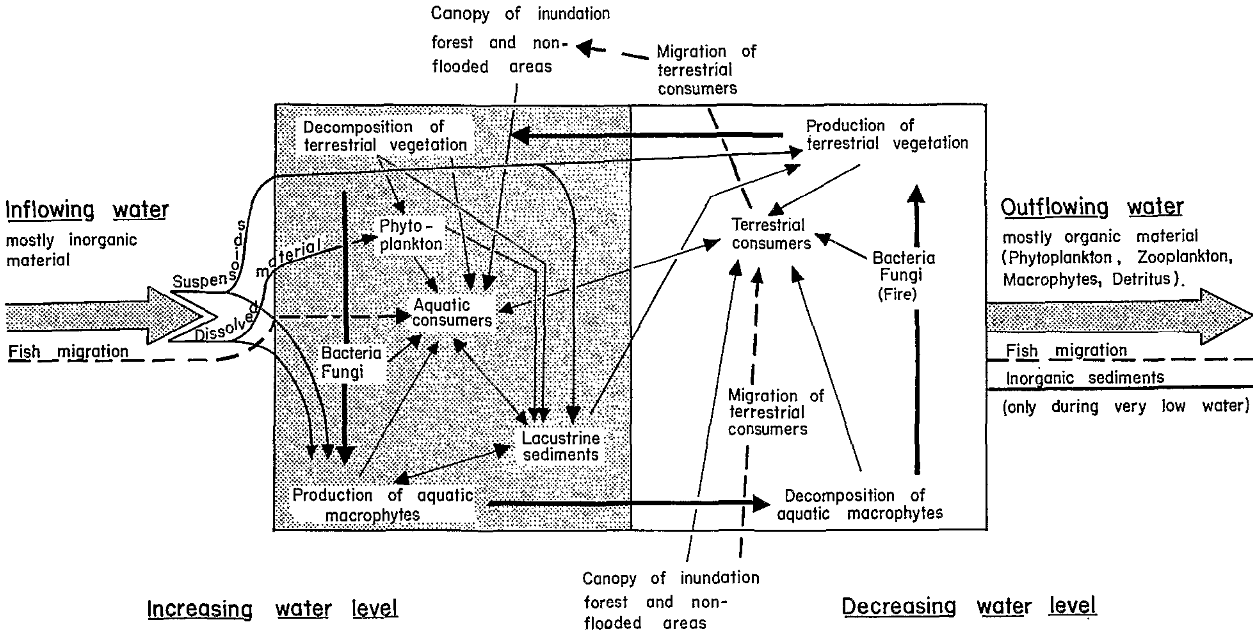


FIG. 3. — Schematic graph of the nutrient cycle and food webs in the várzea of the middle Amazon during high and low water levels

In addition to the nutrient transfer there is an energy transfer, which influences and considerably complicates the food-webs of the várzea. Fruits and seeds of the floodplain-forest are very important food-items for many Amazonian fish species, and these contribute considerably to seed dispersal (GOTTSBERGER, 1978; GOULDING, 1980). In addition, during flooding terrestrial invertebrates are eaten by fish to a considerable degree. During periods of low water, many fish become isolated from the main river, die as the pools dry out, and are eaten by herons, cormorants, vultures and other fish feeders. The small aquatic invertebrates are eaten by terrestrial predators, such as ants moving from the tree canopy to the drying ground. Seeds of aquatic plants are important food items for fishes and birds.

The most important producers of the system, the herbaceous plants, are directly consumed only to a very limited extent. This is astonishing insofar as they represent a high quality food for consumers, containing only small quantities of cell wall fraction but considerable amounts of mineral nutrients and 10-12 % protein (HOWARD-WILLIAMS and JUNK, 1977). Such low consumption of plant material is explained by the low numbers of herbivorous vertebrates like manatees, capybaras and turtles. Formerly these animals occurred in great numbers in the várzea, but populations have been greatly reduced by hunting. Obviously, they have not been replaced in the food-chain by other herbivorous animals. It is therefore possible that man, by hunting, has interfered considerably in the foodwebs of the várzea.

The energy stored in large amounts of herbaceous plants and leaves of the trees from the floodplain forest thus chiefly passes through the detritus food-chain. Certain plant species, whilst alive, may, for chemical, structural or nutritional reasons, be unpalatable to grazing animals. After death, the material becomes increasingly homogeneous. Plants, untouched by grazing animals may later provide favourable substrates for a detritus food-chain (HOWARD-WILLIAMS and JUNK, 1976). Consequently detritus feeders are very frequent in Amazonian foodplains, both in terms of individuals and in terms of species. This is well documented for fish. Most of the numerous members of the family Curimatidae are mud feeders and some of them are important species for human consumption, e.g. the Jaraqui (*Semaprochilodus* spp.) and the Curimata *(Prochilodus nigricans)* (fig. 4). From system-analytical points of view, flood-plains in general and so the várzea in particular, show characteristics of immature ecosystems (MARGALEF, 1968; ODUM, 1971). This is a result of the dominating influence of an abiotic factor, in this case the water-level fluctuation, which, inhibiting further evolution of the system, keeps it in an immature stage (pulse stability, ODUM, 1971). The high rates of production and

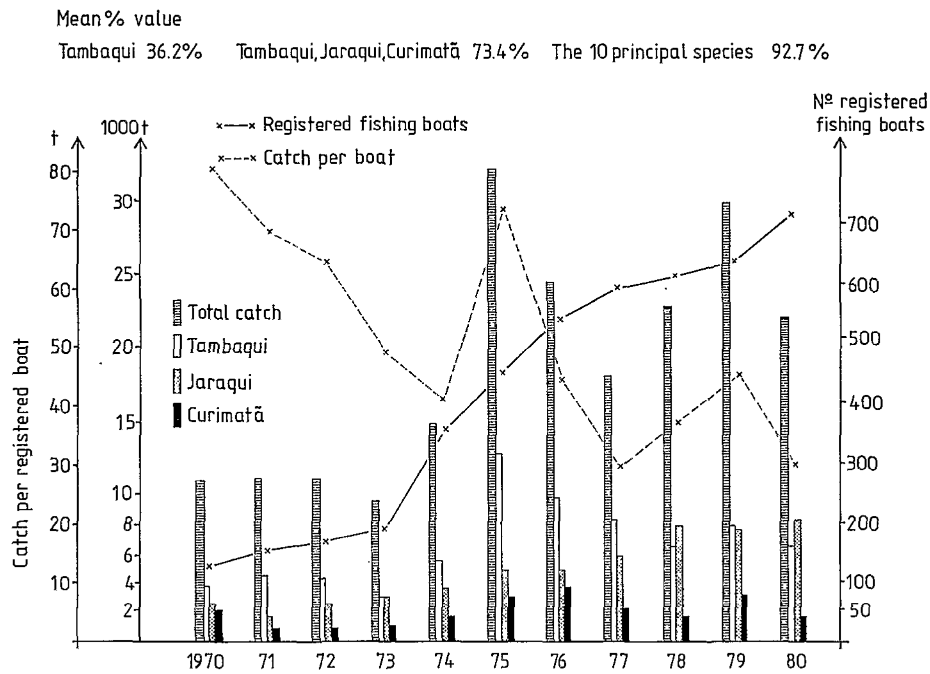


FIG. 4. — Total fish landings and principal species, number of fishing boats, and relationship between total landings and fishing boats in Manaus from 1970 to 1980. (Tambaqui: *Colossoma macropomum*, Jaraqui: *Semaprochilodus* spp., Curimata: *Prochilodus nigricans*). (Data: SUDEPE, Manaus)

decomposition, and the great energy and nutrient losses which are characteristic for such systems are especially well developed in the várzea.

5. ACTUAL UTILIZATION OF AMAZONIAN FLOODPLAINS

The floodplains of the big white-water rivers of Amazonia have been used extensively by man for many centuries. In recent times, agricultural activities have increased around the centres of colonization which develop in the form of small towns, principally along the Amazon itself. Remote areas are utilized only for fisheries and timber exploitation, due to the lack of services needed for colonization. The floodplains of black-water rivers have to be considered as areas of low production potential because of the low concentration of nutrients. This is reflected in the extremely low population density along these rivers. Floodplains of clear-water rivers can be considered as somewhat more productive. However, there is no doubt that above all the floodplains of white-water rivers, the várzeas, have to be considered in any discussion about increasing food production in Amazonian wetlands.

5.1. **Fisheries**

The high productivity of white-water rivers and adjacent várzea is shown by the fisheries (JUNK and HONDA, 1976; PETRERE Jr., 1978a, b; BAYLEY, 1981). The Rio Negro, for instance, a big black-water river passing by Manaus, contributes only about 5 % of the whole catch sold at Manaus market. The much smaller Rio Purus, a white-water river, contributes about 20 % even though it is far away from the city (JUNK and HONDA, 1976). Traditionally, fish is one of the most important sources of animal protein for the population of central Amazonia. In Manaus the *per capita* consumption per year is 55 kg for the low income-groups. In medium and high income-groups it decreases to 51 kg and 38 kg, respectively, because they can afford meat which is more expensive (GIUGLIANO *et al.*, 1978). The total catch of inland fisheries was estimated in 1977 to be about 85 000 t in the Amazonas State and about 150 000 t in the whole Brazilian Amazon region (BAYLEY, 1981). These data indicate the fundamental importance of the inland fisheries for the food supply of the Amazonian population. Statistics show that the total quantity of fish, registered on the market of Manaus, has doubled during the last ten years (fig. 4). The population has also doubled during this time, increasing from 312 000 in 1970 to 642 000 in 1980. The total amount of fish is sufficient to guarantee the supply of Manaus, however short term shortages may occur due to the great seasonal fluctuations in the fish catch. Fisheries depend heavily on the water level, which influence quantity, distribution and behaviour of the fishes.

Tambaqui *(Colossoma macropomum)*, jaraqui (*Semaprochilodus* spp.) and curimata *(Prochilodus nigricans)* form about 75 % of the catch sold in Manaus. Alone the tambaqui represent 36.2 % of all the fish, sold in Manaus, on a 11-year average (fig. 4). Considering there are about 1 300 described fish species, and about 2 000 estimated ones, in Amazonia, this type of fishery is highly selective. Since 1970 the number of registered fishing boats has increased, however since 1975 the number of fishing voyages has decreased, because of high costs of ice and fuel. Total catch per fishing boat has decreased, whereas catch per fishing voyage has shown a slight increase since 1978 (fig. 4, 5). A detailed study of the catch per effort exists only for 1976 (Petrere Jr., 1978a, b). A long term analysis is therefore not possible.

According to Petrere Jr. (1978a, b); Smith (1979) and Bayley (1981), the stocks of the highly requested big species are strongly reduced within a radius of some hundred kilometres around Manaus, and in the Madeira river (Goulding, 1979). Considering that the fishing boats are fishing increasingly in very remote areas of Amazonia, it is presumed that this highly selective fishery will not be able to increase the catch in the long-term.

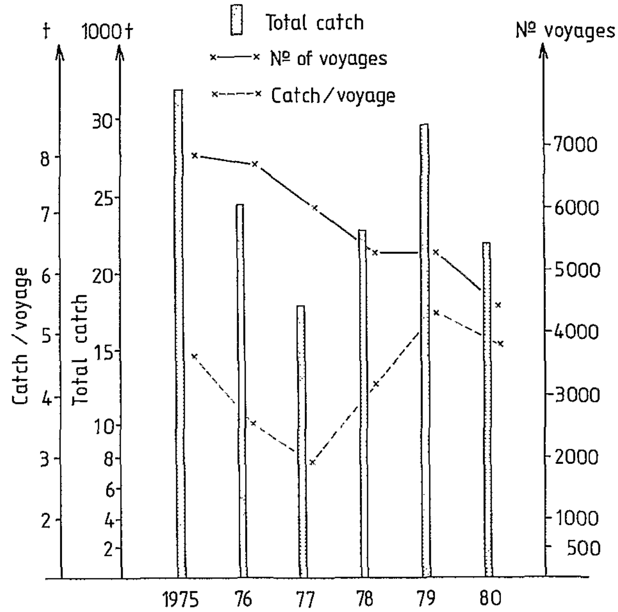


Fig. 5. — Total fish landings, number of fishing voyages and relationship between total landings and fishing voyages in Manaus from 1975 to 1980 (Data: Sudepe, Manaus)

5.2. Agriculture and animal husbandry

Agriculture and animal husbandry in the várzea are very difficult to quantify, because the existing statistics do not differentiate between non-floodable areas (terra firme) and floodplains. Detailed information exists only about the production of jute *(Corchorus capsularis)*, which is mostly cultivated in the várzea. Production of jute fibre in 1977 reached about 25 200 t in the Amazonas State (Ibge, 1977).

During periods of low water the drying beaches of the várzea are used for the cultivation of vegetables, corn, manioc, beans and melons. On the highest areas bananas are grown and small quantities of rubber trees, cacao and fruit trees. However, the total amount of food produced by agriculture and animal husbandry in the State of Amazonas is insufficient to supply the 650 000 inhabitants of Manaus. Considerable amounts of food have to be imported from the south of Brazil (Giugliano *et al.*, 1978). On the other hand short term overproduction of vegetables and fruit occurs, for example of water melons, an indication of the distinctive seasonal character of agricultural utilization of the várzea. Cultivation of paddy rice was started experimentally several decades ago around Belém in the Amazon mouth area. Camargo (1949) indicates a yield of 3,5-5 t/ha per crop without the use of fertilizers. These promising results and the abundance of several endemic species of wild rice in the várzea indicate that suitable conditions for its growth exist. However, paddy cultivation has been developed to a limited extent in the várzea, mostly in the coastal area. Several years ago a spectacular large-scale experiment of paddy cultivation was started at the mouth of the river Jarí, a tributary of the Amazon, about 500 km upstream of Belém. This project is using modern technology, large-scale dyke construction and pumping systems for flood regulation. In the beginning, 2 crops per year of 6-7 t rice each were reported (Alvim, 1978). Apparently these numbers have decreased to 4-5 t during recent years (Schubart, *pers. comm.*). The economics of such a type of paddy cultivation have not yet been estimated. Animal husbandry in the várzea is concentrated mostly on cattle (Sternberg, 1966). The rural populations raise pigs, ducks and chicken for their own needs. Waterbuffalo, which have been raised for many decades in great numbers on the island of

Marajó, at the mouth of the Amazon (57 000 in 1970) are scarce in central Amazonia because of a food preference for cattle meat and milk. The total number of waterbuffalo in the State of Amazonas was estimated as about 2 500 in 1977 (IBGE, 1977).

6. POTENTIAL AND PROBLEMS OF UTILIZATION OF THE VARZEA

There is no doubt among agronomists that the agricultural potential of the várzea is underdeveloped. On the other hand, it is obvious that the necessary supporting services e.g. transport, electricity, schools, hospitals, etc., of the várzea are insufficient in most places, and nonexistent in remote areas. A programme for intensive utilization of the várzea therefore has to be combined with sufficient scientific, technical, administrative and financial help (PETRICK, 1978). It has been shown in the previous sections that from an ecological point of view, the várzea is better suited to agricultural development than the non-floodable terra firme. This is due to better soils, the yearly influx of nutrients during flooding and the intrinsic high production rates of the system. The system is adapted to permanent rapid natural changes (destruction) of biotopes by erosion and sedimentation processes including great losses of organic material. In general this leads to a much higher regeneration capacity and a much shorter regeneration time of most várzea biotopes compared with terra firme forest. However I want to stress that this generalized conclusion is not true for all organisms living in the várzea, as is seen by the strong reduction in numbers of highly specialized long-living animals, like the manatee and turtles, due to hunting and in recent times the reduction of some fish species.

6.1. Fisheries

The existing fisheries concentrate on a few species, most of them big and needing several years to reach maturity, like tambaqui *(Colossoma macropomum)* and pirarucú *(Arapaima gigas)*. On the other hand, there exist many small species which reproduce after one or two years. Greater use of these small, short life-cycle species could considerably increase

TABLE I

Recorded and theoretical yields from the middle and upper Amazon basin in Brazil, 1977. Theoretical values are based on data from African rivers (according BAYLEY, 1981)

Region	River	Recorded yields (t)	Theoretical yields (t) "Normal" floodplains[a]	"Extensive" floodplains[b]	Conductivity (µmhos cm at 20 C°)
1. Upper Amazonas	Amazonas	21.000	13.500	40.600	61-79[c] 40-69
2. Rio Madeira	Madeira	7.800	14.900	14.900	71-97
3. Lower Solimões	Solimões	9.600	4.200	12.700	61-79[d] 71-100[e]
4. Upper Solimões	Solimões		28.450	85.400	120-194[f]
	Purus		24.200	24.200	31-63
	Juruá		25.300	25.300	31-73
	Japurá		5.800	5.800	11-120
	Iça		2.100	2.100	16-24
Subtotal		43.600	85.900	142.800	
5. Negro	Negro	3.200	6.200	6.200	6- 9
Totals		85.200	125.00	217.000	

[a] "Normal" floodplains are less than 1 % of the basin area. Yields are based on catch (t) = 0.0033 (river length in km) , from Welcomme (1976).
[b] "Extensive" floodplains are 1.8 - 2.3 % of the basin area, and have yields about three times those of "normal" floodplains (Welcomme 1976). If floodplain status was in doubt, yields based on "normal" floodplains were used
[c] Unless otherwise noted, conductivity values are for river mouths and are calculated from Gibbs (1967) with his 0.7 conversion factor.
[d] Unpublished data from Rio Solimões near Manaus. Values ranging from 15 to 500 have been recorded from floodplains and lakes influenced by the lower Rio Solimões.
[e] From Rio Solimões near Rio Purus outlet (Gibbs 1967).
[f] From Rio Maranon (Gibbs 1967).

the catch. According to BAYLEY (1981) and considering data from African floodplains (WELCOMME, 1979) a total yield of 300 000-350 000 t/year is realistic for the whole Amazon basin (tab. I). However since most of the species occur in mixed stocks, an intensive utilization of the small species may result in a strong reduction of the bigger ones, e.g. tambaqui and pirarucú which are highly priced and economically very important. The management of these species will be very difficult and may only be possible through total prohibition of fishing for several years in large areas, but, the effect of such a management programme has not yet been studied.

All plans to increase the agricultural utilization of the várzea have to consider the fact that the whole area is used by the fish during high water for spawning, shelter and feeding. Many Amazonian fish species including the tambaqui *(Colossoma macropomum)*, the most important species on the Manaus market, are fruit and seed feeders. A large-scale deforestation of the floodplain forest could lead to marked depletion of the stocks of fruit feeding species. Additionally, deleterious effects of pesticides used in agriculture may have an influence on the fish fauna, either directly by poisoning the fish or indirectly by poisoning aquatic invertebrates, subsequently eaten by the fish. Flood control measures may interrupt feeding and spawning migrations. On the other hand, useful side-effects are possible. For example the quicker recycling of nutrients stored in the vegetation by domestic animals could lead to an increase of phytoplankton, zooplankton and fine detritus. In this case, domestic animals would replace the great native herbivores of the várzea now greatly reduced by hunting.

In any case, it is to be expected that agriculture and animal husbandry will have an effect on the fish stocks. There is thus a great need for detailed studies and interdisciplinary planning of agricultural utilization in the várzea to avoid strong unwanted side-effects on fish stocks. A more general problem affecting agriculture, animal husbandry and fisheries may arise in the future, if increasing industrialization of the Amazon basin causes water pollution by resistant toxic substances. Such substances would also be deposited on the floodplain during high water, poisoning crops, domestic animals and the fish in the affected areas for a long time.

6.2. Fish culture

Considering the rapid population growth even a non-selective fishery industry cannot provide a sufficient supply of fish in the long term. There is therefore a need for the development of aquaculture in Amazonia. This has recently been started, but there is no tradition of aquaculture in the region and our knowledge about Amazonian fish species for aquacultural purposes is very limited. However, results of experiments with Amazonian fish in the north-east of Brazil and recently at INPA, are promising. Some of the species with high commercial value, like tambaqui *(Colossoma macropomum)* and matrincha (*Brycon* sp.) seem to have great potential for aquaculture because of their rapid growth, herbivorous or omnivorous habits and high tolerance of low oxygen concentrations. The reproduction of these species in captivity still presents problems and fingerlings cannot be produced in sufficient number. Studies on the cultivation of indigenous species are of special importance, because they offer a better alternative to exotic species like tilapias. An uncontrolled spread of exotic species could have deleterious effects on the native fauna.

In fact the use of the várzea for aquaculture is difficult because of the high water level fluctuations, and many experiments are needed to develop appropriate techniques, which can be used successfully. On the other hand the small swampy valleys beside the little creeks could be adapted for fish farming. Experiments with ponds supplied by ground water have shown a production of 5-8 t/ha/year with additional feeding (WERDER and SAINT-PAUL, 1978; SAINT-PAUL and WERDER, 1980; SAINT-PAUL, 1981). Such areas cannot be used for agriculture or cattle rising, and fish-culture therefore offers an additional possibility for food production. Compared to cattle farms, fish farms occupy relatively small areas, producing high yields. According to FEARNSIDE (1979) potential cattle weight gain in central Amazonia is 26,2 kg/ha/year. The hydrological conditions of the area are subjected to tewer modifications by fish farms, because deforestation is less and water is stored in the ponds. The shallow lakes in Roraima also have great potential for aquaculture, but all these water bodies are extremely poor in nutrients and would require an additional food supply or fertilizing for successful fish farming. In the future, an increasing number of reservoirs and large man-made lakes could offer additional possibilities for extensive fish culture development.

Besides increasing the total amount of fish available, fish culture will diminish the large oscillations in the availability of fish, which are caused by the seasonal character of the inland fisheries. It will help both to avoid temporary shortages of the product on the market and or stabilize prices.

6.3. Agriculture

A realistic evaluation of the agricultural potential of the várzea is actually not possible because of the lack of detailed maps. Most of the crops are dependent on the duration of the dry period, and there are no data available about the total dry area suitable for agricultural purposes at different levels of inundation. In this context, the need of an adequate number of stations on the Amazon and its large tributaries for water level monitoring has to be stressed. Because of the enormous catchment area it takes several weeks for the water to flow from the upper courses to the mouth. Computerized water level data may in future permit prediction of water level for several weeks, at times of great importance for planting and harvesting, animal husbandry and fisheries.

The success of agriculture in the várzea will depend to a large extent on the development of methods to utilize the benefits of the regular inundations, e.g. natural fertilization and the elimination of parasites and weeds. The high natural productivity of the system is a result of the flooding. Therefore floodplains cannot be treated in the same way as non-floodable land. It would be disastrous to try to avoid the inundations by large-scale dam construction. Rather, it is necessary to introduce or to develop varieties of crops adapted to floodplain conditions, such as short life cycle or flood-resistant varieties.

As elsewhere in tropical agriculture, large-scale monoculture in the várzea must be avoided because of the problem of pests and parasites. According to the topography, areas are subjected to flooding periods of different duration, soil structure and quality differ, and ground water levels vary. High areas require irrigation during the dry season, while low ones require drainage (Petrick, 1978). Clearly therefore the cultivation of a variety of crops is called for. Camargo (1948) suggested combined utilization of várzea and adjacent terra firme, using the várzea mostly for annual crops and the terra firme for forest agriculture.

Recently, EMBRAPA (1) has carried out experiments with small scale rice plantation near Manaus. This type of approach is much better suited to the prevailing ecological conditions, the existing services and the social organisation of the rural population than is the large-scale Jarí experiment. Results are not yet available.

In future, increasing importance will have to be placed on the cultivation of jute. Since the price of petrol is rising strongly, synthetic fibres are becoming more expensive and the market for natural fibres is thus improving. Nothing is known about the potential of the várzea for the cultivation of flood resistant tree species for timber and cellulose production.

6.4. **Animal husbandry**

The big advantage of the várzea for animal husbandry to the terra firme, is the existence of large quantities of high quality aquatic and terrestrial endemic grasses. In addition to having a protein content of 10-12 %, relatively high concentration of mineral nutrients and high production rates (Howard-Williams and Junk, 1977), they show flood resistance and reduced susceptibility to pests and parasites. There are many possibilities of increasing the available pasture by substituting low quality plants by high quality endemic grasses e.g. by *Echinochloa polystachya*.

In this context an experiment should be mentioned which began about 40 years ago on a large lake near Belém in the mouth of the Amazon. The levee was cut in several places, connecting the lake directly with the river by short artificial channels. The resulting strong influence of river water led to intensive sedimentation processes and land formation inside the lake, and those areas colonized by grasses were used as pastures. Unfortunately, only little information is available about this experiment (Camargo, 1958).

Cut grass is used as cattle fodder only during high water. Aquatic grasses *(Echinochloa polystachya, Paspalum repens)* are cut by machetes from small boats and then transported to the farms. Experiments with modified reed cutting machines could lead to more intensive utilization of the enormous areas covered with high quality aquatic grasses. During the dry season, pasture utilization is complicated by the fact that the herbaceous plants of the várzea have a very high reproduction and distribution potential. Therefore, intensive utilization of the pastures by highly selective animals like cattle quickly leads to substitution of high quality fodder plants by plants which are not eaten by the animals. Compared to cattle, waterbuffalo eat a greater variety of plants and are themselves better adapted to the periodic inundation. Their different behaviour and capacity to cross even large water channels, requires different husbandry and makes their propagation in Amazonia difficult. Efforts to increase their numbers in central Amazonia have to be considered as a positive step. Pigs could be reared in much greater numbers

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(1) EMBRAPA = Brazilian Institute for Agricultural and Cattle Research.

in the várzea, if aquatic plants such as the water hyacinth *(Eichhornia crassipes)* were more extensively used as fodder. The same is true for ducks.

Animal husbandry in the várzea will always suffer during periods of high water level. Dry places in which the animals can shelter from the inundation have to be built. In addition, food availability is low when the water level begins to fall because the terrestrial plants need some time to colonize the drying beaches. However, as has been shown, the food supply can be improved by increased utilization of aquatic plants. The usual protection of animals against flooding is by the construction of artificially elevated platforms or floats, so-called 'marombas'. During recent years the transport of cattle from the várzea to the terra firme by ships during highest water has increased (STERNBERG, 1966). The proposal of Camargo, to use the várzea for the growth of annual crops and terra firme for forest agriculture can thus be extended to animal husbandry. The várzea is used as pasture for most of the year and adjacent terra firme as a temporary refuge during periods of highest water level. The economic feasibility of this type of combined utilization of várzea and adjacent terra firme on a large-scale has yet to be demonstrated.

7. CONCLUSIONS

Considering available data concerning floodplains in general and Amazonian floodplains in particular, it has to be said that our knowledge of the ecology of such areas is very limited. However the information available does show that floodplains differ considerably from other wetland ecosystems. Because of the periodic change of land-water boundary caused by the strong water level fluctuation they are highly dynamic systems. Floodplains should be considered as intermediate between open and closed systems, receiving nutrients from the river, transforming these through internal cycles into organic material and transferring part of them to the river again. If sufficient nutrients are available the alternation between aquatic and terrestrial phase results in high production and decomposition rates.

In Amazonian floodplains the nutrient supply is relatively high in the várzea of white-water rivers whereas it is low in the igapó of black-water rivers and intermediate in the igapó of clear-water rivers. A more intensive utilization of the várzea by agriculture and animal husbandry is therefore advisable.

From an ecological point of view such an increase of activities can be recommended if the methods and techniques used do not greatly inhibit the annual flooding, but utilize its beneficial effects. Large-scale flood control would deteriously modify the character of the system diminishing its high natural production capacity.

It is to be expected that agricultural activities will have a considerable impact on the fish stocks but this must be studied carefully because of the great economic importance of inland fisheries in Amazonia in producing a protein supply for the local population. The yield of inland fisheries could double if, instead of the highly selective fisheries, more intensive use of stocks of small species was developed. However, to guarantee a long term fish supply, fish culture should be developed using creeks and swampy areas on the terra firme as well as lakes and reservoirs.

There is no doubt that effective utilization of the várzea will depend on the availability of services as well as extensive scientific, technical, administrative and financial assistance. To what extent such assistance can be offered will depend on the long term development strategies of the Brazilian government. Intensified utilization of the várzea by agriculture and animal husbandry could shift some of the colonization activities currently concentrated on nutrient poor, and fragile, terra firme forest systems to the relatively nutrient rich and more resistant floodplain system, opening up additional possibilities for food production and settlement in Amazonia.

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