OBSERVATIONS ON AQUATIC MACROPHYTE DYNAMICS IN THE RESERVOIR OF THE BALBINA HYDROELECTRIC POWERPLANT, AMAZONAS STATE, BRAZIL

Ilse WALKER[1], Roberto MIYAI[2], M. D. Amaral de MELO[3]

ABSTRACT — Between 1991 and 1995 aquatic macrophyte composition was observed in the lower part of the reservoir of the hydroelectric power plant of Balbina (Amazonas, Brazil). After closure of the dam in 1987, vegetation cover - mostly *Eichhornia crassipes* - was high, but was not quantified. After 1990 it declined rapidly with a characteristic succession pattern: *Eichhornia* → *Utricularia* + Cyperaceae → *Salvinia* . The Cyperaceae, and many other less dominant species, were mostly associated with drift wood, produced by the decomposing, emergent forest. Comparison of the chemical data of the Uatumã river before the construction of the dam (1983) with those of later years (1989 - 1995) suggests that the succession was the result of a relatively mild and short period of eutrophication, followed by declining nutrient levels. Annual variation of water levels, followed by aquatic and terrestrial decomposition of the marginal vegetation, may allow for the maintenance of relatively productive vegetation belts along the shore lines of islands and inundated stream valleys.

Key-words: Hydroelectric powerplants, Amazonas, Balbina, water plants.

Observações Sobre a Dinâmica de Macrófitas Aquáticas no Lago da Usina Hidrelétrica de Balbina, Amazonas, Brasil.

RESUMO — Entre 1991 e 1995 a composição das macrófitas aquáticas do porção inferior do reservatório da hidrelétrica de Balbina foi observada. Após o fechamento do lago pela barragem em 1987 a cobertura do lago por macrófitas aquáticas, principalmente por *Eichhornia crassipes*, foi alta, mas não existem dados quantitativos. A partir de 1990 a redução da cobertura foi rápida, e notou-se uma sucessão nítida e consistente em diversas áreas do lago: *Eichhornia* → *Utricularia* e Cyperaceae → *Salvinia*. As ciperáceas e outras plantas menos dominantes foram associadas com madeiras flutuantes provenientes da floresta emergente em decomposição. O monitoramento contínuo das condições químicas da água (1983 - presente) sugere que a sucessão é o resultado de um período relativamente curto de eutrofização, seguido por um declínio rápido do teor de nutrientes. Devido as variações anuais do nível d'água, a faixa marginal das ilhas e dos igarapés inundados é caraterizada por solos relativamente ricos, graças à decomposição periódica de plantas terrestres inundadas na cheia, e de macrófitas aquáticas na seca. Portanto, espera-se que o lago, com suas milhares de ilhas e igarapés inundados, sustente uma certa produtividade pesqueira, apesar do baixo nível de nutrientes do lago.

Palavras-chaves: Usinas hidrelétricas, Amazonas, Balbina, macrófitas aquáticas

I. INTRODUCTION

This paper is an attempt to synthesize various independent, and often incomplete, observations, which accumulated in the course of time in various reports and in the field notes of the authors. The reason to combine these diverse data arose from the first authors project on the trophic structure of the aquatic fauna along the marginal zones of islands, which started in 1991.

The closure of the dam of the hydroelectric power plant of Balbina (Amazonas State, Brazil) in 1987 turned a hilly landscape under primary tropical rain forest,

---

[1] Instituto Nacional de Pesquisas da Amazônia (CPEC/INPA) Caixa Postal 478, 69.083-000 Manaus, AM, Brazil

[2] CPA Samuel, 79.900 Porto Velho RO

[3] UHE Balbina, 69.736-000 Balbina AM. Brazil

ACTA AMAZONICA 29(2): 243-265. 1999.

dissected by hundreds of forest streams, into an enormous lake with some 3000 islands. The formerly shaded banks of forest streams transformed into the sunny margins of islands and of wider, open bays. The objective of the project is to compare the foodweb of these new ecosystems with the foodweb previously established for forest streams (Walker, 1987; 1991). It was soon apparent that much of the aquatic fauna was associated with aquatic macrophytes, notably with the originally ubiquitious *Eichhornia crassipes*, the presence of which was accepted as a matter of fact. Yet, macrophyte cover changed rapidly during the period of field work (1991 - 1995). Thus, originally casual observations on macrophyte presence became more and more elaborate in order to get a rough quantitative estimate of plant cover, the analysis of which indicated a consistent process of species succession. Hence, limnological data were reviewed in order to examine possible relations between changing water quality and plant succession. This documentation should, in turn, assist in the future interpretation of the data on animal community structure in the sampling areas.

Furthermore, man-made lakes in general (Lowe-McConnell, 1966), and in tropical regions in particular (Lentvaar, 1967; 1974), are a topic of major concern. This includes operational problems of power plants caused by macrophyte cover (Torre & Riveira, 1992) and adverse, ecological effects, such as degradation of water quality, O_2- depletion, loss of forest areas and of wild life (Tundisi, 1989), and possible global effects via emission of greenhouse gases (Fearnside, 1995). The data of the present communication might thus be of use for ecological evaluation of future hydroelectric projects in the Amazonian region.

II. OBSERVATION AREAS, MATERIAL AND METHODS

1. Balbina lake and the islands chosen for observation

Balbina lake is the reservoir of the Balbina hydroelectric power plant (Presidente Figueiredo County, Amazonas state) and was created by the construction of a dam across the Uatumã River in 1987. The drainage area of the Uatumã, a northern tributary of the lower Amazon some 220 km east of Manaus, is 70,600 km^2, the northern-most 18,862 km^2 of which feed the Balbina lake. The area actually inundated is 2,360 km^2. However, owing to the low declivity of the river and to the hilly landscape, the area affected by the lake extends over some 6,800 km^2 (maximum length = 155 km, width = 75 km), which includes approximately 3000 islands of different sizes, shapes and altitudes. The final water level of the lake was reached in 1989, with a maximum depth of ca. 30 m and an average depth of 7.4 m. The whole basin is covered by primary tropical rain forest with a mean tree height of 30-35 m. Hence, with the exception of the former river and stream channels, the lake is characterized by dead emergent forest. In the lower positions of the former river and stream valleys, only the tree crowns emerge above the water surface. However, to reach the islands, one may have to navigate for hundreds of meters through dead forest of 20-25 m height. The last tree species to die out was *Macrolobium* sp.

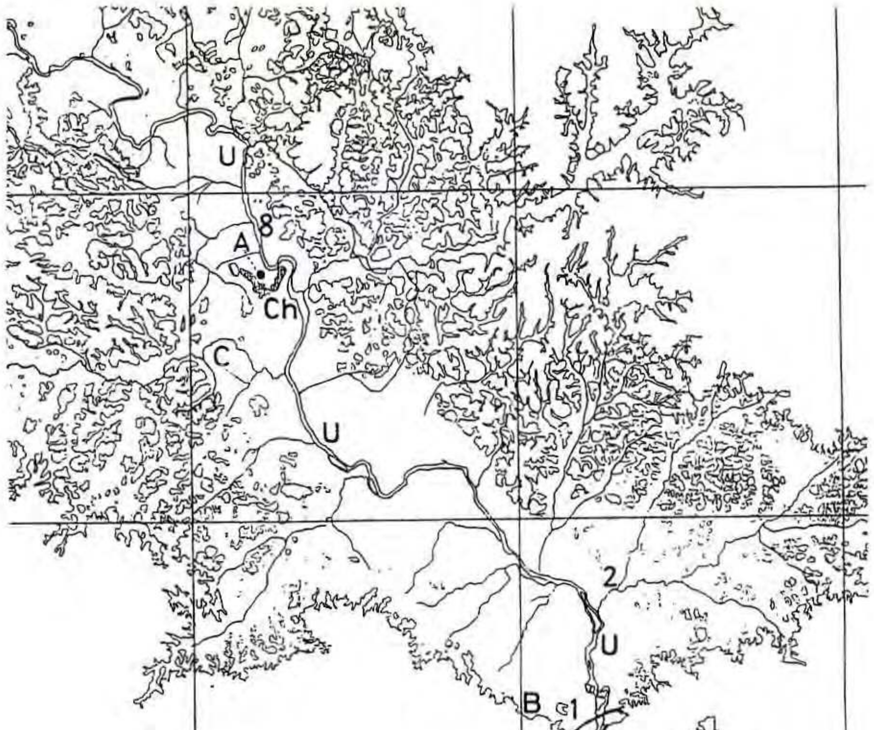
(Leguminosae; April 1991, lower ca. 50 km of the lake). By the end of 1995, some 50% of the larger tree trunks (> 25 cm DM) and ca 90% of the thinner, emerging woods were broken, and the trunks still standing had lost most of their branches.

Along the shores, trees that formerly grew on well-drained soils found themselves in water- saturated soils. Consequently, these trees died as well and were replaced by fast-growing secondary species adapted to hydromorphic soils. Thus, all shores are characterized by a belt of dead forest, with dense tree falls and by thick secondary growth.

The islands chosen in 1990 for biological observations were the "Serra do Chocador" and the "Ilha das Aranhas" (Fig. 1).

The Serra do Chocador is a steep, ~90 m (above lake level) high range of hills of ca. 1 km^2 in area, situated ca. 35

Figure 1. Map of lower Balbina lake with the former river courses. U: Uatumã River. 1: water sampling station M1 adjacent to the dam. 2: sampling station M2 in the channel of the eastern tributary Igarapé da Esperança near the Ilha das Aranhas (too small to appear on the map). 8: sampling station M8. Ch: island Serra do Chocador with observation area A (dot) mentioned in the text. B: area where the quadrat samples were taken (Tab. 3). C: former western tributary Igarapé Caitetu. Black area in south-east corner: Balbina Village. Distance between coordinate lines: 20 km.



km upriver from the dam. Before the closure of the dam it blocked the course of the Uatumã river and forced it to change direction, whence its name: "Shock Range". The larger tributary stream Igarapé Caitetu drained its southeastern area.

The Ilha das Aranhas is a small (~20 ha), flat island, emerging a mere 2 - 3 m above the water surface. It lies between the junction of the Uatumã and the major eastern affluent Igarapé da Esperança, ca. 5 km upstream from the dam. It has no official name on the map, and we called it "Spider Island" because of the extraordinary density of spiders in its marginal forest belt. The island is, in fact, the flat top of a former range, and a narrow constriction forming a small bay is actually the head area of a steep valley, with water depths of 8-15 m at 15-20 m distance from the shore.

The hydrological sampling stations M2 (Igarapé da Esperança) and M8 (ca. 4 km upriver from the Serra do Chocador) are those nearest to the islands under observation. They were chosen before the closure of the dam and are thus situated in the area of the river channels.

2. Observation of aquatic macrophytes

On both islands, a marginal stretch of some 250-350 m along the S/E shores was chosen for standardized observations and collection of material.

Observations of aquatic plant cover (Tabs. 2A, 2B) refer generally to two areas, a proximal belt along the water line with a relatively high plant density, which diminished often rather abruptly in the more distal areas (= distal belt).

Distances of ≥10 m were estimated as multiples of canoe length (= 6.4 m), when rowing, or very slowly motoring, from, to and along the islands' margins.

Plant cover was estimated by visual impression only. The approximate percentage of plant cover of several sub-areas, limited by conspicuous dead trees or by floating trunks, were averaged along a shore stretch of at least 150 m. Considering the size and the complexity of the study areas, and the difficulties and the dangers of navigating through dense forests in an advanced stage of decomposition, with drift wood and dead trees impeding straight-line movement, these visual approximations were the only method to arrive at some more or less useful data on plant cover in the overall area. The data in Tables 2A and 2B thus include an error of ca. " 7% in the range of 25-75% plant cover, and less for % cover outside this range.

Between September 1995 and March 1996 some exact quadrat samples were taken in an area of 100% cover (Fig. 1, Site B). The contents of the quadrats (50 cm x 50 cm) were separated according to plant species, dried and weighed. Plant dry weight was determined by oven-drying at 90°C until the weight stabilized.

3. Hydrological sampling methods

Hydrological data were collected at fixed sampling stations (M1 - M20) along the Uatumã and in major tributaries starting in 1983. After the closure of the dam, data were collected at monthly intervals, with occasional gaps during certain periods and in certain areas. These irregularities are mentioned in the respective tables. With the exception of the 1983 data (Tab. 1, before the closure of the dam), only stations M1 (near the dam), and the previously mentioned sta-

Table 1. Water quality before the closure of the dam across the Uatumã River. Igarapé (= Stream in Portuguese) Caitetu and Igarapé da Esperança: streams draining areas near the later islands "Serra do Chocador" and "Ilha das Aranhas". Given are means ± standard deviation and/or range of 7-9 sampling stations along the Uatumã, and n = 1-5 readings in single stations in the stream channels.

		Conditions of surface H_2O in 1983		
Period		Uatumã	Igarapé Esperança Ilha das Aranhas	Igarapé Caitetu S. do chocador
Temp.	Feb-Mar	32.20 ± 0.58		
°C	May-Jun	27.69 ± 0.38	28,0°	27,0°
pH	Feb-Mar	5.29 ± 0.28	4.80 ± 0.30	4.60 ± 0.28
	May-Jun	4.44 ± 0.24	n = 5	n = 4
µS/cm	Mar-Jun	19.56 ± 4.92	13.07 ± 2.79	11.3 ± 0.94
		Range:	n = 4	n = 4
		10.9 - 30.0		
O_2	Feb-Mar	6.14 ± 0.48	3.7 - 6.2	4.0 - 5.2
mg/l	May-Jun	4.69 ± 0.21		
Ca^{++}		0.46 ± 0.25	0.18 ± 0.18	0.45
mg/l			n = 2	n = 1
NH_4	µg/l	25 - 55	45 - 57	46
PO_4	µg/l	5.0 - 8.5	12.5	18.0

tions M2 and M8 were considered in the presentation of the results.

Temperature readings were taken at the hydrological stations and occasionally at the plant sampling sites, with mercury thermometers (accuracy ± 0.5°C).

Water samples were collected in Van Dorn sample bottles and were processed in the limnological laboratory of the power plant (Eletronorte, Balbina) adjacent to the dam, at room temperature (25°C). Oxygen titres were determined by the Winkler method. For pH readings and nutrient determinations (PO_4, NH_4) equipment made by Micronal S/A, São Paulo was used: Potentiometer Model B-375 (pH and conductivity) and Spectrophotometer Model B-382 (nutrients). The methodologies followed the guidelines of Strickland *et al.* (1972) and Golterman *et al.* (1978).

4. Soil analysis

To gain some indication of soil fertility, nine soil samples were collected in March 1993, during the low water period, along the islands' margins.

Ilha das Aranhas: Two samples at 1.0 - 1.5 m from the water line, at 7 m horizontal distance, and a third sample at the equivalent position on a small, adjacent island (= samples IWA, IWB, IWC); two samples 4 - 5 m further inland, with a height of ca. 0.4 m above the actual water level (= samples IHA, IHB).

The same sampling layout was maintained along the shore of the Serra do Chocador (= samples SWA, SWB near the water line, SHA, SHB higher up the bank), however, the higher positions (4-5 m from the water line) corresponded to ca. 1 m above the actual water level, because the Serra do Chocador has much steeper slopes than the Ilha das Aranhas. All higher positions, though, were inundated during the previous high-water period (May-Sept. 1992).

The samples consisted of top soil (1-15 cm deep); live roots and larger wood debris were removed before analysis.

The samples were processed in INPA's Agronomy Department. The methods of analysis followed the "Manual of methods of soil analysis of the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA)". The criteria of soil quality in Table 10 are adopted from Vieira (1975).

5. Documentation

Unless otherwise indicated, the data presented were extracted from the following unplublished reports (see also literature cited for specifrcations): (1) Convênio Eletronorte, MCT, CNPq, INPA (1982), Relatórios setoriais; (2) Eletronorte, Monasa, Enge-Rio (1986), Estudos ambientais do Reservatório de Balbina, Relatório diagnóstico, Convênio Eletronorte, CNPq, INPA, Limnologia, J.S. Ribeiro; (3) Camargo & Miyai (1983); (4) Froehlich, Figueiredo & Miyai (1993); (5) Databank of the Limnological Laboratory of the UHE Balbina (R. Miyai, M. D. Amaral de Melo, A. Figueiredo); and (6) Field notes on lake vegetation (I. Walker).

III. FIELD OBSERVATIONS, RESULTS AND DISCUSSION

1. Conditions before the construction of the dam

The Central Amazonian Region, which includes the Uatumã basin, is subject to marked annual seasonality of temperature and precipitation. Between 1978 and 1984 the mean annual minimum of rainfall, occurring in August, was 107 mm; the month of maximum precipitation was April, with a total monthly mean of 353 mm; total mean annual precipitation amounted to 2294 mm. Average monthly air temperatures ranged between 26°C and 28°C, the mean minimum between 1978 and 1984 was 20.9 in March and the maximum 37°C in November. Mean daily insolation was 5-7 hours/day, with a minimum of 3 h/d in April.

Evapotranspiration by the forest was estimated at 1200-1500 mm/year, and thus contributes some 50 - 70% to the annual precipitation budget. The frequent, local and short noon/afternoon rains during the dry season are due to the forest's evapotranspiration. Clouds begin to form at about 9:00 am, invariably over the land (not over the lake as observed after the closure of the dam!), and may reach rain storm dimensions between 11:00 and 14:00 (see also Leopoldo *et al.*, 1987).

The Uatumã river responds with a time lag of several weeks to this seasonality. Mean discharge at the dam site from 1977-1984 was 570 m^3/sec; in 1984 it varied from 197 m^3 in November and 1127 m^3 in June.

All following data refer to the region above the dam site. Water depths in June reached 10 m in certain stretches, with maximum flow speed 1.1 m/sec. Under these conditions, solid suspended matter was 13-16 mg/l (dry weight). With the above mentioned discharge, this means that approximately 1.5 - 5.5 tons of solid matter were transported down-river per hour. Erosion and sedimentation processes in Amazonian blackwater rivers are thus not negligible (Walker, 1995).

Surface water temperatures also reflected seasonality (Tab. 1). The relatively high temperatures in Feb/March indicate that the water must have been stagnating over extended areas. Normal surface temperatures of running water in Amazonian rivers are usually below 30°C (Walker, 1995). Owing to flat topography, the wide meandering river undoubtedly had open lake-like regions.

Water chemistry (Tab. 1). The upper part of the Uatumã drainage basin is on the Precambrian crystalline Guyana shield, while in lower positions along the upper valleys and in the lower basin tertiary fluvial sediments, argilites and arenites predominate (Barreiras and Amazonas formations). Both rock types are poor in cations, and weathering of the sedimentary rocks under forest cover gives rise to clay and sandy soils. Podzolization processes, moreover, result in acid black water, i.e. waters which are rich in dissolved orange-brown humic substances (Leenheer, 1980; Chauvel *et al.,* 1987; 1996). Parts of the north-eastern basin, however, drain areas on marine, sedimentary rocks (Trombetas formation), which are rich in Ca, Mg, Na, and K. For this reason, the Uatumã - although a nutrient poor, acid blackwater river - has a relatively higher conductivity and higher Ca^{++} levels than other amazonian black waters and the Rio Negro, the latter with a conductivity of 9 - 11µS /cm and a Ca^{++} content of 0.3 mg/liter (Ungemach, 1972; Schmidt, 1972).

Aquatic macrophytes: There are few references to aquatic macrophytes in pre-1987 reports. The semestral report of January-July 1985 shows five photographs of the Igarapé da Esperança with dense covers of *Eichhornia crassipes* and with floating meadows (Graminea). The 1986 report mentions the presence of *E. crassipes*, *E. azurea* and *Paspalum repens* (Graminea) in the Uatumã, *P. repens* being one of the grass species in the floating meadows of the Amazonas. Thus, the somewhat better nutrient conditions of the Uatumã and of its major tributaries allowed for the growth, accumulation and dispersal of aquatic macrophytes, which are so conspicuously absent in the Rio Negro and its central Amazonian blackwater tributaries.

2. OBSERVATIONS ON AQUATIC MACROPHYTES AFTER THE CLOSURE OF THE DAM (1991 - 1995).

2.1 Long-term changes: the probability of true succession

Eichhornia crassipes was the only species that called one's attention in 1991. Indeed, photographs taken in 1988/89 show the wide, open lake above the dam completely covered by *Eichhornia.* Excluding "trunks with vegetation", we find that along both islands an originally wide vegetation belt shrank to 1-3 m width between 1991 and 1995, and the originally dominant *Eichhornia* diminished to only sporadic presence.

Utricularia sp. (see p.12) was

Table 2. A Aquatic macrophyte belts along the shores of the two islands "Ilha das Aranhas" (A) and "Serra do Chocador" (B). P = width of proximal belt, from water edge to its distal boundary. D = distal belt; given is distance from water edge to approximate distal boundary. >x: further out than x meters. +: sporadic presence only (≤1%). -: absence specifically stressed in field notes. *Only two *Eichhornia* plants seen. ** The formerly floating trunks had sunk, and their vegetation formed floating patches.

		Width of vegetation belts (m) with %plant cover																			
Year	type of vegetaation	Feb		Mar		May		Jun		Jul		Aug		Set		Out		Nov		Dec	
		P	D	P	D	P	D	P	D	P	D	P	D	P	D	P	D	P	D	P	D
1991	P/D m									20-50	>50			30-50	.100	8	.50	≤25	50	5-10	50
	Eichhornia %									50	+			50	1-2	60	50	40	≤10	40	≤10
1992	P/D m													5	≥10						
	Eichhornia %													20	+						
	Utricularia %													+							
	Aniseia %													+		+					
	Trunks + veg %													+							
1993	P/D m					3	≥50					2	≥3								
	Eichhornia %					70	+					45	+								
	Utricularia																				
	Aniseia %					+						45	+								
1994	P/D m			10	≤10			3	≥10	10-15	>15	≤6	≃18	5	25			2-6	10		
	Eichhorniia %			+	+			≤2	+	5	-	5		50				40-70	20		
	Utricularia			+	+			+	+	+		5		15-20							
	Aniseia %																				
	Trunks+veg.			+				+	+	+			90	+	100			+	65		
	Cyperaceae			80				≤20		95				15-20							
	Salvinia									+									1-2		
1995	P/D m	10-25	>25	2-6	≤15					1	≤12			10-20	>20			2-4	20		
	Eichhornia %		-	1						+				+	-			-	-		
	Utracularia				+									+				≤15	+		
	Aniseia %									+				+	-						
	Trunks+veg %	100		90	4					+	50-80			50	+			50**	50		
	Gramineae %									+											
	Salvinia %			1						10-30				≤5				≤5	+		

Cont.

Table 2. B

		Width of vegetation belts (m) with % plant cover																			
	type of	Feb		Mar		May		Jun		Jul		Aug		Set		Out		Nov		Dec	
Year	vegetaation	P	D	P	D	P	D	P	D	P	D	P	D	P	D	P	D	P	D	P	D
1991	P/D m									10	≥50									5-15	50
	Eichhornia %									10-20	+									30	5
1992	P/D m											5	100	5	15						
	Eichhornia %											20	+	40	+						
	Utricularia %											+									
1993	P/D m					2-3	≥10					2	.500								
	Eichhornia %					40-70	+					80-100	+								
	Utricularia					+															
	Aniseia %					+															
	Trunks+veg. %					+															
1994	P/D m			5	>5			5	<5	10	>10			3	10			10	>10		
	Eichhorniia %			+	+			+		45	+			40-60	10			+	+		
	Utricularia			+				10		45											
	Aniseia %																				
	Trunks+veg.									10				20	20			+	+		
	Cyperaceae							10													
1995	P/D m	20	>20	1-2	.100					1-3	>3			1.5	1.5			2	>2		
	Eichhornia %	+	-	+	-					+	-			+				*	-		
	Utricularia	-								20-50	-			20				+			
	Aniseia %																				
	Trunks+veg %			+	+					15-20				20-50	+			100**	-		
	Cyperaceae %																	10			
	Gramineae %									+											
	Salvinia %			+	-					10-70	-			20				+			

noted in 1992 and reached substantial cover by 1994.

Salvinia was definitely absent on both observation sites until July 1994, nor was it noted in any other place we visited. By July 1995 it was the prevalent species in the narrow plant belts along both islands.

Cyperaceae were seen on widely dispersed floating trunks all over the areas of the dead submersed forest; they were explicitly recorded in 1992 within 30-50 m from the water edge along the Ilha das Aranhas. In 1993 Cyperaceae appeared along the shore of the Serra do Chocador, and they became the dominant vegetation on the Ilha das Aranhas. In 1995 the Cyperaceae were no longer itemized in the records, because they were invariably associated with decomposing floating trunks, or so it appeared at the time.

Trunks with vegetation. The decomposing forests in the lake (ca. 2000 km^2) and on the hydromorphic soils along the lake and island shores, resulted in an increasing frequency of tree falls between 1991 and 1994, and thus in large numbers of floating trunks (including large branches). In the lake, the trees suffer aquatic decomposition below the water surface, and aerial decomposition above, with, owing to seasonally changing water levels of 1.5-3.0 m, a transition zone exposed to both processes. Apparently, this zone decomposes fastest, or, more precisely, the zone just above the highwater mark (visible by a color change), which never suffers O_2 - deficiency under water and still benefits from high air humidity during the dry months: most trees and thick branches broke off near the highwater mark. This zone is also preferred by the termites *Nasutitermes* sp.: of a total of 89 nests counted in September 1995 on standing trunks of 5-25 m height above the highwater mark, 43 were within 1 m above the mark. Also, several trees were noted with dense fungus belts just above this mark (Fig. 2).

In 1994, floating trunks, driven by south- easterly winds, accumulated along the SE- exposed shores of both islands. By September 1994, the Ilha das Aranhas became virtually inaccessible from this side. Several factors may have contributed to this relatively sudden accumulation. First, the water level was comparatively high in June/ July 1994, the stumps of the broken trees were thus largely inundated, and this freed the water surface for drift wood. Second, south-easterly winds are relatively strong during the rainy season (January-May). Third, strong winds break relatively larger quantities of still standing trees. Frequent breaking of trees before August 1994 was confirmed by the observation that ca. 40% of the floating trunks along the distal belt of the Ilha das Aranhas in November 1994 were still devoid of vegetation, and, in September 1994, ca. 20% of the trunks along the Serra do Chocador. Similar conditions were noted in September 1995.

The vegetation colonizing drift wood. Decomposing logs drift on the water surface for months, if not for years, and they get colonized by a characteristic vegetation, (Fig. 3) which, when fully developed, may reach 40-80 cm in height. Examination of mostly bare trunks in Sept. 1995 showed that

Figure 2. Dead forest during the low water period in September 1995. *Nasutitermes* sp. colony above the dark lower segment that marks the high water level.

Figure 3. Floating trunk with vegetation and *Salvinia* in the vegetation belt of the Serra do Chocador island.

colonization occurs prevalently via seeds, dispersed by wind and water currents, and caught in the crevices of the bark and wood. These spaces contained the seedlings of most of the species listed below. Most species are semi-aquatic, and form under-water rhizomes. This leads to "creeping" colonization of logs in dense accumulations.

Lycopodium sp. (Cryptograma); *Pityrogramma calomelanos* (L) Link (Pteridophyta); normal habitat: open areas with sand, rocks and pebbles. *Xyris* sp. (Xyridaceae, Monocotyledonae, INPA Herbarium Nr. 341). Superficially resembling Cyperaceae habitus, with a terminal spherical inflorescence and yellow flowers.

Cyperaceae: *Scirpus cubensis* Poepp & Knuth, with conspicuous spherical inflorescence. Normal habitat: flood plain forests; forms aquatic rhizomes. *Scleria macrophylla* Prest. Normal habitat: lake and river margins, temporarily inundated areas. Forms aquatic rhizomes. *Torulinum odoratum* (L) Hooper. Normal habitat: marshlands and open areas along roads (Amazônia). Forms aquatic rhizomes. *Fimbristylis capillaris* (L). Benth. Dark, green, ca. 5-10 cm high, semi-aquatic, forms dense floating carpets upon inundation. Normal habitat: terra firme to inundation forests in open areas, along water edges.

Gramineae: *Panicum laxum* Sw. Also found along the shores of the lake of the Curuá-Una hydroelectric power plant (Pará State), and on the várzea island Marchantaria near Manaus. Forms aquatic rhizomes. *Panicum chloroticum* Nees. Reported from the edge of the Tapajós river. *Hymenachne amplexicaulis*, noted in 1995 only.

Dicotyledonae: *Ludwigia hyssopifolia* (Onagraceae). *Aniseia martinicensis* (Convolvulaceae), creeper of forest edge that invades the open shore with stranded woods. Upon inundation at higher water levels it forms aquatic stolons which then colonize drift wood and upright dead trunks. *Eclipta prostrata* (Compositae), with small, white flowers, aquatic rhizomes were not observed.

Utricularia sp., possibly *U. gibba* L. V. The INPA Herbarium contains a single specimen from marshlands in Mato Grosso. Thin (<1 mm DM) 5-8 cm long stems carry 1-3 yellow flowers with a corolla length of ca. 10 mm. The flowers were frequent on bare trunks in September 1995, and were noted as well on earlier occasions. The invariably very thin flower stems distinguish the species from *U. foliosa*. The vegetative parts form dense sub-aquatic mats which may adhere to floating logs and to the under-water parts of upright dead trees.

Eichhornia crassipes is often associated with driftwood, mostly because it may get entangled with smaller branches. Furthermore, the flora of the floating trunks (mostly Cyperaceae) penetrate the *Eichhornia* roots by aquatic stolons, and thus fix the plants to the floating trunks. In places with dense drift wood (Ilha das Aranhas 1994/95), *Eichhornia* gets caught in the interstitial spaces.

This list is by no means complete, but it contains the most conspicuous species listed between 1992 and 1995.

The pattern of succession. The sequence of prevalent species between 1991 and 1995, namely *Eichhornia* → Utricularia + Cyperaceae → *Salvinia*, and the narrowing of the vegetation belts indicate true species succession as a result of changed limnological conditions. Not only was this sequence concordant between the two islands, but occurred in other places as well, albeit at different paces:

Site A (Fig. 1): In this shallow area behind the Serra do Chocador, *Eichhornia* persisted at high density until late 1994. By July 1995, it had all but disappeared; the surface was clear of water plants, but there were scattered floating trunks with Cyperaceae. *Salvinia* was noted along the edge of a nearby small island and along the NW-shore of the Serra do Chocador (Fig. 4).

Site B: Water depth in this wide bay behind the dam is 2.5-3.0 m, and approximately three hectares of the water surface were completely covered by *E. crassipes* as late as March 1995. Approaching the area again in September, this still seemed to be true, yet on the site *Scirpus cubensis* (Cyperaceae) was found to have massively invaded the area. Their stolons, with few roots at each node, stabilized the tall and slender plants by growing through the massive, mostly dead *Eichhornia* roots intermingled with *Utricularia* (*gibba*?). The presence of driftwood between the water plants suggests that *Scirpus* might have arrived on floating trunks.

Uatumã valley: Occasional observations referring to the forest lining the Uatumã channel, recorded when motoring to the Serra do Chocador, suggest the same plant succession. In

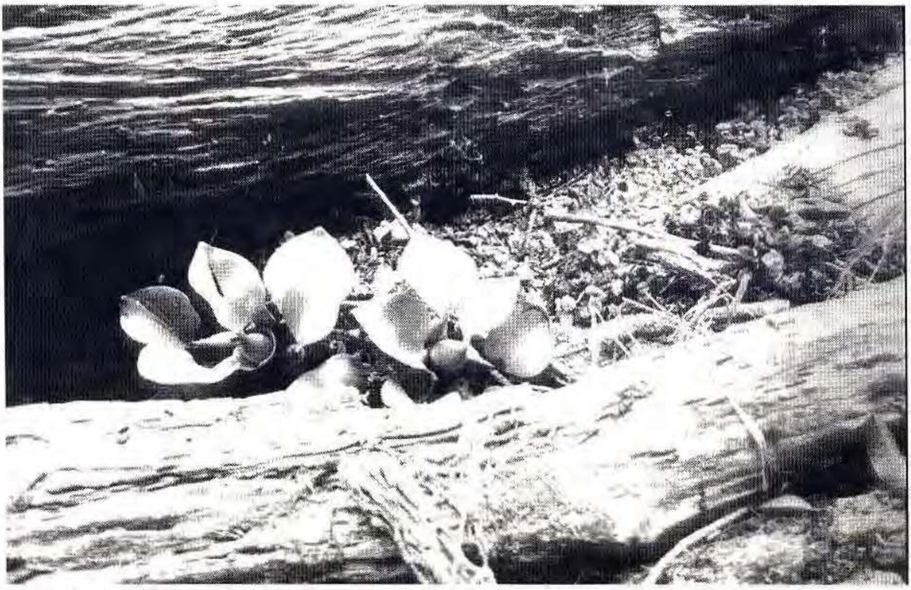


Figure 4. Stranded trunks, *Eichhornia* and *Salvinia* on the shore of the Serra do Chocador island (Sept. 1995).

May 1993 some 2 or 3 *Eichhornia* plants or small patches per hectare were noted; in September 1995 there were less than a dozen on the whole journey. In March 1994, *Utricularia* cover was estimated at ca. 5%; almost every tree was surrounded by *Utricularia* mats. In September 1995, *Salvinia* was seen for the first time floating in the Uatumã channel. The density of floating trunks with vegetation was estimated only once, in March 1995, at 0.5-1.5 trunks/ha.

Plant dry weight: The relation of shoot : root weight is indicative of plant quality in *Eichhornia* (Gopal, 1987); ratios of < 50% indicate growth stress.

In September 1994, these ratios were 41.6 ± 7.8% (n = 10) along the Ilha das Aranhas, 32.2 ± 6.3% (n = 5) along the SE-shore of the Serra do Chocador, and 36.5 ± 7.0% (n = 5) on Site A (behind the Serra do Chocador).

The quadrat samples taken on Site B (Tab. 3) show the drastic decline of *Eichhornia crassipes* in the area. As most of the November 1995 material was lost, sampling was repeated in March 1996. It was impossible to completely disentangle the various species; consequently small quantities of Cyperaceae roots and of *Utricularia* increase the total *Eichhornia* weight by a maximum of 1-2%. Most of the *Eichhornia* roots were dead. The leaves had long petioles and small blades, as is characteristic of stressed plants (Gopal, 1987; Da Silva & Esteevs, 1993). Besides *Scirpus cubensis*, the Cyperaceae include a small fraction of *Fimbristylis* sp (0.5-3%). *Salvinia* was only present in few small fronds with relatively small leaves. In contrast to *Utricularia*, *Salvinia* and *Eichhornia* seemed to survive better along the edge, near the open water; (t- test, edge versus interior (1996): for *Eichhornia*, (green

Table 3. Plant dry weight (g) of quadrat samples (Q1, Q2 for two replicates, 50 cm x 50 cm). Ed = edge of overgrown area; In = ca 4 m inside. Asterisk: Total *Eichhornia* weight, see specification in text; Q2, November 95: material lost in oven accident.

Macrophytes; Dry MWeight (g)						
Data	*Eichhornia*			Cyperaceae	*Utricularia*	*Salvinia*
Q	Total* g	green leaves g	green leaves %			
Sep. 95						
Q1	273.3	62.9	23.0	160.0	13.2	0.24
Q2	377.3	50.0	13.3	180.3	12.0	0.27
Nov. 95						
Q1	483.2	64.1	13.3	69.0	9.4	1.83
Q2	439.6	-	-	-	-	-
Mar. 96						
Ed. Q1	750.0	20.2	2.7	258.2	5.2	0.31
Ed. Q2	467.9	70.2	15.0	228.8	2.1	0.81
Mar. 96						
In. Q1	325.4	7.5	2.3	231.1	26.7	0.0
In. Q2	216.7	2.4	1.0	222.9	24.1	0.11

leaves) and *Utricularia*, $P < 0.01$). Increase of Cyperaceae and *Utricularia* between 1995 and 1996 (interior quadrats): $P<0.02$).

Plant succession and limnological conditions.

Succession of aquatic macrophytes in Amazonian hydroelectric reservoirs is linked to the transition of fluvial to lacustrine conditions with an intensive phase of eutrophication (Tundisi *et al.*, 1993; Froehlich *et al.*, 1993). As it is economically not feasible to remove the forest in remote regions prior to inundation, decomposition of the immersed vegetation in the more oxygenated upper strata (epilimnion) results in a massive release of nutrients, while deeper waters are anoxic. The temperature regime also changes. In the following, data are summarized on the conditions of Balbina lake after the final water levels were reached in 1989, and they are compared to the conditions in 1983, before the construction of the dam.

pH: Between 1988 and 1991, pH varied between 5.3 and 7.0. Between 1992 and 1995, variation was reduced to 5.8 to 6.8, and such variations occurred within single months, as in June 1994 at station M2, for example (5.9 - 6.7). In 1995, pH stabilized between 6.1 and 6.6. in 0-5 m depth, the lowest value in deep water was 5.5. Thus, closure of the dam resulted in reduced acidity ($P<0.01$, t-test, surface water), but between 1991 and 1995 there is no variation that correlates with plant succession. According to Esteves (1988), elevation of pH is a general feature of man-made lakes.

Conductivity (Tab. 4): The closure of the dam resulted in mild eutrophication (1983 versus 1989, $P<0.10$, t-test), followed by a consistent decline of conductivity ($P<0.01$), thus indicating reduction of nutrient levels. Even in deep water (8-20 m) conductivity declined from an annual maximum of 92 µS /cm in 1989 to 55 µS /cm in 1993/94.

Table 4. Surface conductivity. Means and standard deviations of annual minima and maxima; n = number of years. *: Station M1: 2 readings per month; Stations M2 and M8: bi-monthly readings; Maximum at station M8 was taken on January 4, 1996.

		Surface Conductivity, µS/cm		
Years	Means of annual values	Sampling Stations		
		M1	M2	M3
1989	Minima	14.30±3.20	14.93±0.87	12.15±0.45
to		n = 3	n = 3	n = 2
1991	Maxima	28.27±4.77	26.57±6.40	19.95±0.75
1992	Minina	13.23±2.04	12.37±1.64	12.36±1.35
to		n = 3	n = 3	n = 3
1994	Maxima	22.67±3.79	18.80±2/64	18.33±2.99
*	Minimum	10.60	10.60	11.00
1995		n = 1	n = 1	n = 1
	Maximum	14.60	12.70	14.90

NH_4 (Tab. 5): The same trend is shown by the NH_4 values, although, surface concentrations in 1995 were still much higher than in 1983, before the construction of the dam. However, values > 1 mg (>1000 µg) were reached only once (M8, 1989/90), while, according to GOPAL (1987), *Eichhornia* needs a minimum of 20 mg/l for optimal growth, i.e. for a shoot ratio >50%. ($P<0.01$ for annual means of 45.6 (1983), 403 (1989), 88.9 (1995) µg/1). PO_4 levels are a further indicator of water fertility. They jumped from < 20 µg/liter in 1983 to maxima of 40-50 µg /l in 1989, and declined again in later years to annual maxima which stayed below 15 µg/l in all three stations; minima of zero were measured on several occasions (all values referring to surface water). The highest level in deep water (< 20 m) was 337 µg /1; by 1994 the maxima stayed below 100 µg/l at all three stations.

All three indicators (conductivity, NH_4, PO_4) of the fertility of surface water display the same trend: increase of nutrient levels after 1983 to a maximum in 1989 and their subsequent decline. According to Gopal (1987) nutrients, and nitrogen in particular, determine the growth dynamics of *Eichhornia* (physical water conditions permitting). In general limnological terms, even the maximum values in 1989 were modest. It is probable, therefore, that the proliferation of *Eichhornia* after the closure of the dam occurred under suboptimal conditions to begin with, and that the fast decline in later years was the result of reduced nutrient levels.

Surface temperature. (Tab. 6). Seasonal low-temperature stress affects the growth of *Eichhornia* and other water plants if air temperatures fall below 20°C (Mato Grosso; Da Silva & Esteves, 1993). In Balbina, mean minimum air temperature is 22°C, and surface water temperatures stay well above this value (Tab. 6). High- temperature stress might be more probable: within dense macrophyte covers, temperatures of 37°- 42°C were measured on several occasions. After 1991, regular seasonality of changes of surface water temperatures faded as

Table 5. NH_4 (µg /l) content in surface and deep (>15m) water. *: no data in 1991 and 7-9 monthly readings only at station M8 between 1993 and 1995.

		NH_4, µg/Liter			
Years	Means of annual values	Station M2		Station M8	
		Surface	> 15 m	Surface	> 15 m
1989-90	Minima n = 2	71 ± 25	554 ± 18	65 ± 15	1221 ± 723
	Maxima	640 ± 90	3762 ± 165	1134 ± 236	2989 ± 352
* 1992-93	Minima n = 2	24 ± 12	449 ±110	67 ± 32	1758 ± 672
	Maxima	378 ± 262	2432 ± 432	501 ± 364	2700 ± 696
* 1994-95	Minima	30 ± 3	303 ± 70	55 ± 22	876 ± 347
	Maxima	223 ± 163	972 ± 466	645 ± 67	1857 ± 159

Table 6. Temperatures of surface water (°C). Months: period in which annual minima and maxima were measured. n = number of years. Range: mean difference with standard deviation between annual maxima and minima.

		Surface Temperatures (°C)		
Years	Values Months	M1 $\overline{X}$ ± SD	M2 $\overline{X}$ ± SD	M8 $\overline{X}$ ± SD
	Minima	27.67±0.47	28.0±1.41	30.25±0.25
1989	n = 3			
	Months	I - IV	I - IV	I - IV
to	Maxima	32.83±0.85	32.17±0.24	34.5±0.5
	n = 3			
1991	Months	VII - XII	VII - XII	VII - XII
	Range	5.17±0.85	4.17±1.65	4.25±0.25
	Minima	29.0±0.0	30.0±0.0	30.17±0.24
	n = 3			
1992	Months	irregular	irregular	II - III
to	Maxima	32.07±0.09	32.33±0.47	33.0±0.0
	n = 3			
1994	Months	irregular	VI - XI	IX - XI
	Range	3.07±0.05	2.33±0.47	2.83±0.24

a consequence of higher minima. These more stable conditions must be due to the eventual consolidation of lacustrine conditions ($P<0.01$ for the reduction of the range between the two periods; Tab.6, t-test).

O$_2$ (Tab. 7): Oxygen depletion as a consequence of eutrophication processes, consuming O_2 for under water decomposition is clearly shown by the drastically reduced minima in 1989 ($P< 0.02$, t- test). Conditions improved in later years, but even in 1995 the minima remained relatively low compared to the 1983 levels of the Uatumã river. Conditions were similar to a depth of ca. 4 m, but in-deep water (8 - 20 m), O_2 values were virtually zero.

Drastic and irregular changes in surface waters, as shown by the O_2-range and, to a lesser extent, by conductivity and nutrient levels, which may display their annual maximum and minimum within a single month, are probably induced by cold fronts breaking in during the southern winter and/or by strong rain storms during the remainder of the year. The cool surface water sinks to the bottom and warmer O_2-deficient and nutrient-rich water moves to the surface, events that are well documented for the flood plains of the Amazon (Santos, 1980), where they cause massive fish kills. Substantial numbers of dead fish floating on the water surface were indeed observed in Balbina on several occasions, but they never reached the massive proportions reported for the Amazon lakes.

In summary, the probable causes of macrophyte succession as observed in the lower part of Balbina lake between 1989 and 1995 are: 1. Decline of nutrient levels, causing reduction of *Eichhornia crassipes* abundance; 2. high frequency of tree falls in the dead forests, causing dispersal and local accumulations of drift wood, and their colonization by a semi-aquatic flora, acid water favoring Cyperaceae; 3. partial occupation of

Table 7. Oxygen (O_2 mg/l) content of surface water. n = number of years; n*= number of monthly readings. Further explanations see Tab. 4.

Years	Mean ± SD of annual values	Surface O_2, mg/L Sampling Stations M1	 M2	 M8
1989	Minima	0.30 ± 0.08	1.97 ± 1.84	2.40 ± 1.10
to	n	3	3	2
1991	Maxima	6.97 ± 0.76	7.77 ± 0.24	8.20 ± 0.20
1992	Minima	1.20 ± 0.28	2.07 ± 1.29	1.70 ± 0.86
to	n	3	3	3
1994	Minima	7.47 ± 0.66	7.90 ± 0.59	7.10 ± 2.08
	Mean ± SD	5.75 ± 1.48	5.30 ± 1.87	5.22 ± 1.19
1995	n*	19	9	6
	Range	1.40 - 8.90	2.0 - 7.70	3.3 - 6.8

the "niche" liberated by *Eichhornia* by species more tolerant of acid nutrient-poor waters, such as *Utricularia* cf. *gibba* and *Salvinia*. Lastly, the following observation may be added: when returning to the areas in March 1996 (in order to replace the lost quadrat samples, Tab. 3) it appeared that on floating trunks, as well as along the terrestrial margins of the islands, various grass species, including those noted previously on floating trunks (p. 12), proliferated at the cost of the Cyperaceae. This may be due to the stabilization of the pH at only very slightly acid values (Tab. 8). Cyperaceae are usually indicators of distinctly acid substrates.

Table 8. Comparison of surface water pH and conductivity (μS/cm) between marginal water along the Serra do Chocador island and the free water at Station M8.

Date	Distance from Land	μS/cm $\bar{X}$ ± SD	 n	pH $\bar{X}$ ± SD	 n
		Serra do Chocador			
III. 1995	0.8 - 1.5m	11.17 ± 0.06	4	6.17 ± 0.05	4
IX. 1995	1.5m	11.57 ± 0.74	2	6.0 ± 0.02	2
		Station M8 Lake			
III. 1995	>50m	11.75 ± 0.05	2	6.0 ± 0	2
VII		11.5 ± 0	2	6.15 ± 0.05	2

There are notewotrthy parallels between the succession pattern for Balbina and of variation of plant cover as documented for the reservoir of Curuá-Una, the first man-made lake in Amazonia (Pará State, near Santarém). The lake surface, covering the drowned forest vegetation, measures ca. 100 km^2, and the water of Curuá-Una river is acid and poor in nutrients, as is the Uatumã. The hydroelectric power plant started operation in 1977. In April and may 1978 large quantities of aquatic macrophytes were recorded, notably *Eichhornia crassipes*, *Scirpus cubensis*, *Paspalum repens* and *Pistia stratiotes* (which, however, was never noted in Balbina). By September 1979 total plant cover of the lake reached 26.7%, and low frequencies of *Utricularia* sp. and of *Salvinia auriculata* were recorded (Junk, 1982). However, in 1987 "only small quantities of macrophytes" remained in the reservoir of Curuá-Una, this as a consequence of falling nutrient levels (Junk & Nunes de Mello, 1987). Owing to the small size and short water retention of the lake (20 -75 days, Junk, 1982), the process of succession was evidently much faster than in

Balbina. Yet, the observations suggest that, depending on initial water quality, general patterns of plant succession might occur in man-made amazonian lakes.

2.2. ANNUAL PERIODICITY OF MACROPHYTE COVER

Annual differences of water levels in the Balbina reservoir vary from 1.5 m to 3 m, with highest levels from May to July and lowest levels from December to February. This results in periodically inundated marginal zones which vary as a function of each island's slope.

There is some indication from both islands (Tabs. 2A, 2B), that the macrophyte belt was widest in July, and that % cover increased during the second part of the year. With falling water levels, the plants nearest to the land get stranded and generally die, as is the case of *Eichhornia*, or they survive and proliferate, as do the semi-aquatic species on stranded drift wood. In late 1994, the *Eichhornia* belt was so narrow that the *Eichhornia* populations dried up completely, and reconstitution could not keep pace with the new invaders, *Utricularia* and *Salvinia*. During low water levels, the terrestrial vegetation of the forest edge invades the shore, including the creeper *Aniseia martinicensis*, which survives the inundation period, and other fully terrestrial species, such as Passifloraceae, various grasses, seedlings of secondary growth etc. The stranded logs either get fixed to the ground by roots, or else, they gain in specific weight: upon re-inundation during rising waters they stay mostly on the ground.

Fertility along the shores. It was expected that the seasonal alternation between decomposition of aquatic plants during the low water period and of terrestrial plants during the high water period would result in higher nutrient levels in the water and soil along the shores. For the marginal water, this does not seem to be the case (Tab. 8).

Soil fertility, on the other hand, is relatively high if compared to the general poverty of Amazonian terra-firme soils (Klinge, 1976). This is at least true for organic matter, K, Na and Ca (Tabs. 9, 10). Balbina lake, thus, seems to conform to pattern, in that the marginal zones of lakes (eulitoral zone, Jorgensen, 1990) with its vegetation is a "collector of nutrients" (Kurata & Kira, 1990).

Table 9. Composition of top soil samples from the shores of the islands, collected in March 1995. Granulometric soil components in % of weight. Means and standard deviations (x±SD) of n = 8 samples from both islands, with the exclusion of the sample SWB (Serra do Chocador, water line, replicate B). *: SWB values outside the range of other samples. Positions see explanation of sample code, Table 11.

Granulometric components: Soil fractions in % weight.

Component Particle size,mm	Clay ≤0.002	Fine silt >0.002-0.05	Coarsse silt >0.05-0.10	Fine sand >0.10-0.50	Coarse sand >0.50	Organic matter H_2O_2-extraction
$\overline{X}$ ± SD %	34.37±12.71	7.41±2.09	4.91±0.87	17.60±2.52	31.55±11.73	4.43±1.69
Range n=8	15.49-55.0	5.75-12.45	3.69-6.67	13.74-20.70	17.16-52.16	2.70-7.90
SWB, n=1	31.4	7.65	0.64*	9.30	20.0	30.89*

Table 10. Fertility of soil samples. Standards for poor, medium fertile and rich soils: from Soil Manual (Vieira 1975). Further explanations see Tables 9 and 11.

Accessiible nutrients: soluble quantities per 100g of soil

Elements	Acidity pH	Ca^{++} mg	Mg^{++} mg	Na^{+} mg	K^{+} mg	PO_4 µg
Mean ± SD	4.63 ± 0.21	0.93 ± 0.77	0.18 ± 0.04	0.20 ± 0.02	0.12 ± 0.04	92.5 ± 8.3
Range, n = 8	4.34 - 4.94	0.20 - 1.46	0.13 - 0.24	0.17 - 0.23	0.06 - 0.18	80.0 - 100.0
SWB, n = 1	4.07	0.69	0.25*	0.41*	0.24*	100.0
Poor soils		< 1.5	< 0.5	< 0.1	< 0.03	< 500
Medium		1.5-4.0	0.5 - 1.0	0.1 - 0.3	0.03 - 0.06	500 - 1000
Rich		> 4.0	> 1.0	> 0.3	> 0.06	> 1000

Considering the islands' terrestrial/aquatic interface with a high rate of plant growth and decomposition, with at least medium soil fertility, yet nutrient- poor waters, it must be concluded that the nutrients, instead of being released into the water, are immediately re- absorbed by the living biomass. The same seems to be true for Amazonian forest streams and their inundation forests: the aquatic food chains depend almost exclusively on the decomposition of the submerged forest litter, yet, conductivity along the water courses declines from 30 - 60 µS /cm in headwater streams to below 15 µS/cm in higher order rivers, in their inundation forests and in the Rio Negro (Walker, 1995).

Shore soil fertility is patchy (Tab. 11): most values of the sample SWB are outside the range of the other 8 samples. Furthermore, the samples in lower positions with a longer period of inundation, seem to be richer than those higher up the slope. This is shown by the samples of the Serra do Chocador. As the Ilha das Aranhas is very flat, the two samples taken further inland suffered practically the same inundation periods and conditions as the three taken near the water edge. Hence, their values were pooled. They are relatively rich in organic matter but poor in cations. It is to be expected that variation between islands, and horizontal and vertical patchiness along each island, may give rise to qualitative and quantitative variation of plant cover along the aquatic/terrestrial interface of the shores of Balbina lake.

CONCLUSIONS

Perhaps rather surprisingly, permanent inundation of the dense rain forest in the relatively shallow reservoir of the nutrient-poor, acid blackwater Uatumã River resulted in only a mild and relatively short-lived phase of eutrophication. Within eight years, conductivity from the surface to a depth of 4-5 m declined to pre-reservoir levels in the lower part of Balbina lake, and O_2- levels were comparable to those of the intact inundation forest of the Rio Negro during high water levels (Irmler, 1975; Walker, 1995). The process was characterized by a specific succession of aquatic macrophytes, which resulted in a narrow vegetation belt along the shores composed of species which tolerate nutrient-poor acid conditions. It is possible, though, that the final elevation of the pH to ≥ 6.0 will allow Gramineae to thrive along the water

Table 11. Differences of soil quality between islands and between sites. Code of sample sites: S for Serra do Chocador; W for position near water line (1 - 1.5 m from water edge); H for higher positions (4 - 5 m from water edge); A and B for replicates taken at circa 7 m horizontal distance. Itemized are the parameters with SWB values outside the range of the other 8 samples. Comments on the samples of the Ilha das Aranhas see text, p. 20

	Site - specific values. Weigth per 100g soil				
Islands:	Serra do Chocador				Ilha das Aranhas
Sites	Near water line		Higher position positions		All 5 sites
	SWA	SWB	SHA	SHB	$\bar{X}$ ± SD
Organic Material g	5.22	30.88	3.17	3.00	4.81 ± 1.98
C g	3.03	17.91	1.84	1.74	2.79 ± 1.09
N g	0.16	0.75	0.12	0.12	0.17 ± 0.07
C/N	18.90	23.90	15.30	14.50	16.58 ± 0.93
Mg^{++} mg	0.24	0.25	0.17	0.22	0.15 ± 0.02
K^{+} mg	0.18	0.24	0.15	0.13	0.09 ± 0.03

edge, rather than the Cyperaceae that dominated until November 1995.

Plant succession essentially involved the emergent decomposing forest, with frequent tree falls, leading to dispersion and accumulation of drift wood, densely colonized by semi- aquatic plant species. Depending on prevalent wind direction, drift wood accumulations might interfere with the water intake of the power plant. In Balbina, south-easterly winds apparently prevented the accumulation of floating trunks in the lowest open part of the lake adjacent to the dam.

Annual variation of water levels with alternating aquatic and terrestrial decomposition of the terrestrial and aquatic vegetation belt along the sun-lit shores may maintain a belt of relatively rich soils along the aquatic-terrestrial interface. If this proves to be true in the long run, productivity of man-made, Amazonian lakes with acid nutrient-poor waters is a function of the relation between the total length of the shoreline and the lake area. If properly managed, Balbina lake, with its several thousand islands and stream bays, may thus continue as an important area of fish production.

ACKNOWLEDGEMENTS

The authors wish to acknowledge the essential help of their staff and collegues: Dr. R. Ghilardi (Eletronorte) and Dr. P. Fearnside (INPA) for critical review and for pertinent suggestions; Dr. M. Bras de Queiroz (INPA) for topographic information on the islands and for the map in Figure 1. Dr. A. Figueiredo (Eletronorte) for processing the limnological data; Dr. J. P. Lescure, Dr. L. Emperaire (ORSTOM/ INPA), Dr. A. Sprada Tavares, C. Freitas, J. Ferreira Ramos and J. Lima dos Santos (Herbarium, INPA) for their assistance in plant identification; Dr. L.A. Gomes de Souza, E. Chaves and S. de N. Moraisi (Dept. of Agriculture, INPA) for the soil analyses; M. J. N. Ferreira, J. B. Santos da Silva (INPA) and Z. J. N. Motta Ribeiro (Eletronorte) for assistance in the field and in the laboratory. Special recognition is due to the "motoristas" which, during all these years, manoevered the canoes through the dense, dead forest in its advanced stages of decomposition, without ever provoking an accident: R. Silva dos Santos Filho (Eletronorte), J.B. Santos da Silva, J. Nunes Palheta and J. B. Sá Rodrigues (INPA). Financial support: INPA, Eletronorte, CNPq.

Literature Cited

Camargo, F.M.; Miyai, R.K. 1983. Estudos limnológicos na bacia hidrográfica do Rio Uatumã. Projeto Balbina: Convênio Eletronorte/INPA. *Relatório Técnico*. Eletronorte, Brasília, DF.

Chauvel, A.; Lucas, Y.; Boulet, R. 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazônia, Brasil. *Experientia*, 43: 234-241.

Chauvel, A.; Walker, I.; Lucas, Y. 1996. Sedimentation related to pedogenesis in the drainage basin and inundation forest of the Central Amazonian stream Tarumã-Mirim. *Biogeochemistry*, 33: 77-95

Da Silva, C.J.; Esteves, F.A. 1993. Biomass of three macrophytes in the Pantanal of the Mato Grosso, Brasil. *Int. J. Ecol. and Env. Sci.*, 19: 11-23.

Eletronorte; Monasa; Enge-Rio. 1986. Estudos ambientais do Reservatório de Balbina. *Relatório diagnóstico*. Convênio Eletronorte/CNPq/INPA. INPA, Manaus, AM e Eletronorte, Brasília, DF. 308 pp.

Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). 1995. *Manual de métodos de análise de solos*. SNLCS, Rio de Janeiro. 220 pp.

Esteves, F.A. 1988. *Fundamentos de Limnologia*. Editora Interciência/FINEP, Rio de Janeiro, 575pp.

Fearnside, P.M. 1995. Hydroelectric dams in the Brazilian Amazon as sources of "greenhouse" gases. *Environmental Conservation*, 22: 7-19

Froehlich, F.; Figueiredo, A.; Miyai, R. 1993. *Caraterísticas físico-químicas de reservatórios na Amazônia: UHE Tucurui e Balbina*. Curso organizado pela Universidade das Nações Unidas, e pela Escola de Engenharia de São Carlos (SP), Universidade de Sao Paulo.

Gopal, B. 1987. *Water Hyacinth*. Aquatic plant studies 1. Elsevier, Amsterdam, 471pp.

Golterman, H.L.; Clymo, R.S.; Ohnstad, M.A. 1978. *Methods for physical and chemical analysis of fresh waters*. 2. Edition. Blackwell Sci. Publ. Oxford, Boston. 217 pp.

Irmler, U. 1975. Ecological studies of the aquatic-soil invertebrates in three inundation forests of Central Amazonia. *Amazoniana*, 5: 337 - 409.

Jorgensen, S. E. 1990. Introduction. *In* : Jorgensen, S.E.; Loeffler, H. (Ed) *Lake shore management: Guidelines of lake management. Vol. 3*. ILEC, UNEP. 173 pp.

Junk, W.J. 1982. Zur Entwicklung aquatischer Macrophyten in Curuá-Una, dem ersten Stausee in Zentralamazonien. *Arch. Hydrobiol.*, 95:169-180

Junk, W.J.; Nunes de Mello, J.A.S. 1987. Impactos ecológicos das represas hidrelétricas na Bacia Amazônica brasileira. *Tübinger Geographische Studien*, 95: 367-385

Junk, W.J.; Robertson, B.A.; Darwich, A.J.; Vieira, I. 1981. Investigações limnológicas em Curuá-Una, a primeira represa hidrelétrica na Amazônia Central. *Acta Amazonica*, 11(4):689-716

Klinge, H. 1976. Bilanzierung von Hauptnährstoffen im Oekosystem tropischer Regenwälder (Manaus)., vorläufige Daten. *Biogeographica*, 7: 59-77.

Kurata, A.; Kira, T. 1990. Water quality aspects. *In*: Jorgensen, S.E.; Loeffler H. (ed.). *Guidelines of lake management. Vol. 3*.ILEC, UNEP: pp. 21-38.

Leenheer, J.A. 1980. Origin and nature of humic substances in the waters of the Amazon River Basin. *Acta Amazonica*, 10: 513-526.

Lentvaar, P. 1967. The artificial Brokopondo Lake of the Surinam River; its biological implications. *Atas do Simpósio sobre a biota Amazônica*, 3: 127-140.

Lentvaar, P. 1974. Inundation of a tropical forest in Suriname (Dutch Guiana), South America. *Proc. I. Int. Congr. Ecol.*

Leopoldo, P.R.; Franken, W.; Salati, B.; Ribeiro, M.N. 1987. Towards a water balance in the Central Amazonian Region. *Experientia*, 43: 222-234.

Ribeiro, J.S.B. 1985. Estudos de ecologia e controle ambiental na região do reservatório da UHE de Balbina. Convênio Eletronorte/CNPq/INPA. *Relatórios setoriais. Vol. 1*: 1-30

Santos, U.M. 1980. Aspectos limnológicos do lago Grande Jutai (Amazônia Central), face as alterações químicas do meio hídrico da região. *Acta Amazonica*, 10: 797-822.

Schmidt, G.W. 1972. Chemical properties of some waters in the tropical rain forest region of Central Amazonia. *Amazoniana*, 3: 199-207.

Strickland, J.D.; Parson, T.R. 1972. *A practical handbook of sea water analysis*. 2 edition. Fisheries Research Board of Canada, Ottawa. 311 pp.

Torre, T.A.; Riveira, G.S. 1992. Problemas de operacion del embalse arsenal por vegetacion muerta. *Anais XX Seminario Nacional de Grandes Barragens*, vol 1: 145-158.

Tundisi, J.G. 1989. Management of reservoirs in Brasil. *In*: Jorgensen, S.B.; Vollenwider, H. A. (eds). *Guidelines of lake management. Vol. 10*. ILEC, UNEC: 155-169.

Tundisi, J.G.; Matsumura-Tundisi, T.; Calijuri, M.C. 1993. Limnology and management of reservoirs in Brasil. *In*: Straskraba, M.; Tundisi, J.G.; Duncan, A. (eds). *Comparative reservoir limnology and water quality management*. Kluwer Acad. Publ. Dordrecht: 25-55.

Ungemach, H. 1972. Die Ionenfracht des Rio Negro, Staat Amazonas, Brasilien. *Amazoniana*, 3: 175-185.

Vieira, L.S. 1975. *Manual da ciência do solo*. Editora Agronômica Ceres Ltda. São Paulo. 2 ed. 464 pp.

Walker, I. 1987. The biology of streams as part of amazonian forest ecology. *Experientia*, 43: 279-287.

Walker, I. 1990. Ecologia e biologia dos igapós e igarapés. *Ciência Hoje* 11/64: 44 - 53.

Walker, I. 1995. Amazonian streams and small rivers. *In*: Tundisi, J.G.; Bicudo, C.B.; Matsumura-Tundisi, T. (eds). *Limnology in Brasil*. Bras. Acad. Sci. and Bras. Limnol. Soc.: 167-194

Walker, I. 1995. Sedimentation in the inundation forest flanking the Central Amazonian blackwater stream Rio Tarumã- Mirim (Manaus, Amazonas State). *Amazoniana*, 13: 237-243.

Aceito para publicação em 04.11.98