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VALUE OF FRUITS AND SEEDS FROM THE FLOODPLAIN FORESTS OF CENTRAL AMAZONIA AS FOOD RESOURCE FOR FISH

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Abstract: Floodplain forests of Central Amazonia are heavily influenced by the periodic fluctuation of the water level. The regular change between terrestrial and aquatic phase in the forests has an impact on fruit-shedding as well as on many fish species: during inundation, which lasts for months, they migrate into flooded forests to feed on fruits and seeds shed by trees and bushes in an area more than 300 000 km² in size. For the region near Manaus, Amazonia, Brazil, we report on: (1) the nutritional value and further chemical details of 19 fruits and seeds of those species used by fish as food, furthermore on an additional 11 species which probably serve or could serve as fish food, (2) the amount of fruits-shed in one biota for 4 selected species, and (3) the percentage of different fish catches with fruits as stomach content. Total annual production of the whole inundated forest can be estimated to be 16 - 53 million tons of fruits, corresponding to a monetary value of the fish production from the floodplains in the range of US$ 320 to 530 million. The idea is discussed that since some of the fruits which are preferred by frugivorous fish are abundant in three different biotae, it could be possible to use them to feed farmed fish. *Accepted 12 December 1996.*

Key words: Amazonia, inundated forest, fruit, chemical composition, fish.

INTRODUCTION

The Amazon and its tributaries have a catchment area of 7.9 million km² and inundate every year at peak flood stage approximately 0.3 million km². Water levels may rise as much as thirteen meters. Within the floodplain area, flooded forests may be inundated anywhere from three to eleven months each year, depending on local floodplain topography and the intensity of the annual floods. There are estimates of 70 000 km² flooded forest in the Brazilian Amazon, or about 0.9 % of the total area (Pires 1972).

Most of the tree and bush species fruit during the high-water period (Ziburski 1990, Colonnello 1991). Ripe fruits fall into the water and keep floating for differing periods of time, which helps hydrochoric seed distribution.

However, for many fish species the inundated forest generally is a natural orchard. It is well known that not only *Colossoma macropomum* (Tambaqui), one of the most consumed fish of the area, but also many other fish species, feed almost entirely on fruits and seeds of the inundated forests during the high-water period (Honda 1974; Silva *et al.* 1977; Gottsberger 1978; Smith 1979; Goulding 1980, 1983, 1989; Saint-Paul 1982; Ziburski 1990). *Colossoma macropomum* has developed a special dentition more similar to a horse than to a fish for this kind of feeding, which makes it possible to open even the hardest pericarps, for example from *Crateva benthami.* Sinking fruits are also eaten, e.g., by ground dwelling fish like *Lithodoras dorsalis* (Bacu pedra). However there is little information on to what extent fish captured in white and black water inundated forests feed on fruits and seeds throughout the year.

More than 500 trees/ha have been recorded for the white water inundated forest, and most of them produce fruits and seeds which are consumed by fish (Campbell *et al.* 1992, Balslev *et al.* 1987, Foster 1990). Fruit and seed production in the flooded forests is much higher than in other forests (Revilla 1991). For example *Astrocaryum jauari* produces 1.7 t of fruit per year and hectare, *Pseudobombax munguba* 2.2 t and *Crateva benthami* 1.9 t. Total production is between 15 and 20 t of fruit and seeds per year and hectare, 60% of which is consumed by the aquatic fauna.

Many studies have considered various aspects of this forest-fish-relationship, mainly in the Central Amazon: Gottsberger (1978), Goulding (1980, 1985) and Goulding *et al.* (1988) related the fruiting

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of some tree species to ichthyochorous propagation; Piedade (1985) and Kubitzki (1985) proved ichthyochory for *Astrocaryum jauari* and *Gentum venosum*; Honda (1974), Saint-Paul (1982), Roubach (1991) and Roubach & Saint-Paul (1994) analysed fruit uptake on the basis of stomach contents; Ziburski (1990) investigated the floating capacity of some fruits and seeds. Goulding *et al.* (1996) estimate 132 000 t to 610 000t of fish per year in the white water, based only on the fruit production of the inundated forests.

This paper considers the chemical composition of 19 fruits of the flooding forests that are consumed by fish, and another 11 of the flooding and the non- flooding area (*terra firme*). The amounts of crude protein, crude fat, crude fibre, crude ash, soluble carbohydrate, energy, phosphates, silicates and polyphenols of the fruits and seeds were measured. Furthermore, timing and amount of falling fruit were spatially analyzed, and stomach content analyses of caught fish in different flooding areas were carried out to determine how many fish of which area feed on different amounts of fruits.

MATERIAL AND METHODS

Fruit species. The following 19 fruit varieties have been proven to be eaten by fish (Honda 1974; Silva *et al.* 1977; Gottsberger 1978; Smith 1979; Goulding 1980, 1983, 1989; Saint-Paul 1982; Ziburski 1990). They are ordered alphabetically according to family:

Scientific Name	Common Name	Family
Annona montana	*Graviola*	Annonaceae
Ilex inundata	*Mongulu*	Aquifoliaceae
Astrocaryum jauari	*Jauarí*	Arecaceae
Euterpe oleracea	*Assaí*	Arecaceae
Pyrenoglyphus maraja	*Marajá*	Arecaceae
Crescentia amazonica	*Cuia*	Bignoniaceae
Pseudobombax munguba	*Munguba*	Bombacaceae
Macrolobium acaciifolium	*Arapari*	Caesalpinaceae
Crateva benthami	*Catoré*	Capparaceae
Alchornea schomburgkiana	*Supiarana*	Euphorbiaceae
Hevea brasiliensis	*Seringa verdadeira*	Euphorbiaceae
Nectandra amazonum	*Loro*	Lauraceae
Eschweilera tenuifolia	*Macacaricujá*	Lecythidaceae
Carapa guianenesis	*Andiroba*	Meliaceae
Cecropia latiloba	*Embaúba*	Moraceae
Psidium acutangulum	*Goiaba araçá*	Myrtaceae
Symmeria paniculata	*Caruaçú*	Polygonaceae
Pouteria glomerata	*Abiurana*	Saporaceae
Vitex cymosa	*Tarumã*	Verbenaceae

It is suspected of another 11 species that they are either eaten by fish or could be used as fish food due to their high nutritional value:

Scientific Name	Common Name	Family
Escleronema species	*Campinarana*	Bombacaceae
Scleronema micranthum	*Cardeiro*	Bombacaceae
Aldina latifolia	*Macucú do Igapó*	Caesalpinaceae
Caesalpinia pulcherrima	*Breu-de-estudante*	Caesalpinaceae
Ipomoea species	*unknown*	Convolvulaceae
Casearia species	*Sardinheira vulgar*	Flacourtiaceae
Cariniana decandra	*Tauarí*	Lecythidaceae
Phtirusa rufa	*Erva-de-passarinho*	Loranthaceae
Enterolobium schomburgkii	*Orelha-de-macaco*	Mimosaceae
Inga species	*Ingá*	Mimosaceae
Eugenia cumini	*Azeitona*	Myrtaceae

Sampling site. The fruits were collected from three different locations in the surroundings of Manaus, in Central Amazonia: a white water forest (*várzea*) on the island of Ilha da Marchantaria (59°58'W, 3°2'S) in the river Solimões, in a black water forest (*igapó*) in the river Tarumã-Mirim (60°17'W, 3°2'S) and on the non- flooded area of the Reserva Ducke (59°59'W, 2°55'S). The white and black water forests have different soil and water qualities. The white water is relatively rich in nutritients and electrolytes in comparison to the black water (Furch 1984). Consequently the soils of the respective white and black water flooded areas vary in their fertility.

Fruit production of four selected species. From May to September 1991, fruit production of four trees species (*Vitex cymosa, Psidium acutangulum, Ilex inundata, Pouteria glomerata*) from the floodplain forests of the Ilha da Marchantaria close to Manaus, whose fruits are known to be eaten by fish, was determined. During the period of fruiting, which was determined as the interval between the appearance of the first and the last ripe fruit, 1 m^2 fruit traps were used. On an average, three trees of each species were sampled with five traps for each tree. Fruits were collected, counted and weighed at weekly intervals.

Fruit collection and preparation. Collection proceeded during various stages of the flooding season between 1991 and 1993. We attempted to collect equally ripe fruit using fruits traps, never collecting fruits that were already lying on the ground, and collecting fruits of one species with similar colour, size and texture. Using a ruler, length x breadth was measured. In the results given, values are standardized.

Fruit-drying was done in Manaus, Brazil (105°C). In Kiel, Germany, the fruits were ground (Retsch mill type ZM1) and separated in pericarp and seeds, or even pericarp, seeds, testa and embryo for the analysis. Fruits with a small sample size, or small physical size, were not separated. Separation is necessary because fish seldom make use of whole fruit (Saint-Paul 1982, Ziburski 1990).

Fruit chemical composition. A classical Weender Analysis, including crude protein, fat, fibre, ash, and soluble carbohydrates (calculated) of the seeds and pericarps was done, following the procedures of the German Agricultural Research Institutes Association (Naumann *et al.* 1976). This is in accordance with internationally recognized proximate analysis, which is still in wide use and which allows easy comparisons, e.g., Boberfeld (1994). Polyphosphates (Anonymus 1969) and phenols (King & Heath 1967) were measured photometrically, the energy with a bomb calorimeter (IKA), and silicates gravimetrically as insoluble by-products of the crude ash.

SEM analyses. Specialized tissues, which enable fruit and seeds to float, were examined with a scanning electron microscope (Leitz SEM 1000). The cross-sections through pericarp and testa of fresh material were dehydrated, transferred on to acetone, dried using the critical-point method and then sputtered with gold.

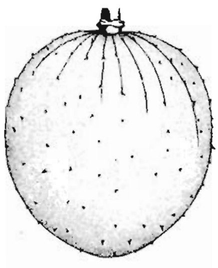
Fish stomach content. A comparative study lasting two years examined the impact of the inundated forest on fishes of a black (Lago Prato, Anavilhanas) and a white water area (Lago Inácio, Rio Manacapurú). Fish were captured by different sized gillnets in 1990 and '91 at low, rising, high and falling water level within and outside the inundated forests for two days each time. The main objective was to find out how important forest plant matter is for frugivorous fish with access to fruits and seeds that fall into the water during the flood. A total number of 20 904 fish from the white, and 5 628 fish from the black water were captured. For the analysis of food habits, stomach content or anterior part of the gut was examined. However, obvious carnivorous species were not considered because of the objective of the investigation.

Of the total number of 239 different species captured on both sample sites over two years, 90 were investigated with regard to their feeding preference. Depending on the water level, this represents in the white water between 35 and 41 species (51–71% of the total catch), and in the black water between 19 and 49 (47–95% of the total catch).

Food items were divided into eight categories: fruit/seeds, allochthonous arthropods, aquatic insects, crustacea/molluscs, fish, zooplankton, algae, and detritus. The occurrence method was employed, for determining the relative importance of the various food items eaten by fishes, by making a simple list of the total number of times a particular food item occurred in the stomach. Taking into account the dominance of the analyzed species within the community, the occurrence of each food item within the community was calculated in percentage.

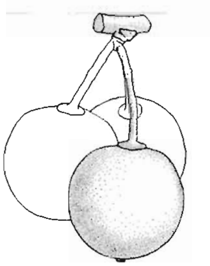
RESULTS

Chemical composition of the fruits. The following illustrations (originals, or taken from Roosmalen 1985) and descriptions are of fruits examined which have been demonstrated to be eaten by fish. Fruits are described in terms of size, type (berry, capsule, pod, drupe, pyx, nut), time of fructification, water content and the relationship of pericarp to seed given in dry mass to dry mass (w/w). The fruits vary a great deal in terms of colour, hardness and size. In general they are characterized by their poorly developed flesh.



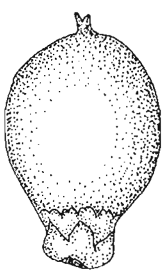
Annona montana – Graviola, Annonaceae (Roosmalen, 1985)

Fruit: many-seeded, brownish-green berry; 9 x 8.5 to 13.5 x 12 cm
Seed: 1.5 x 1 cm; floating for 2–3 weeks
Fructification: April to August
Relationship of pericarp to seed: 1.04 to 1 (w/w)
Water content: 82 %



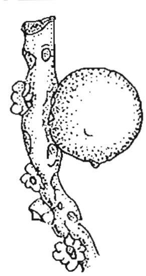
Ilex inundata – Mongulu, Aquifoliaceae;

Fruit: three-seeded, round, black berry; 0.6 to 1 cm; not floating; dispersal endozoochorically by birds
Seed: 0.5 x 0.3 cm; the fruit was not separated for the analysis
Fructification: May to August
Water content: 64 %



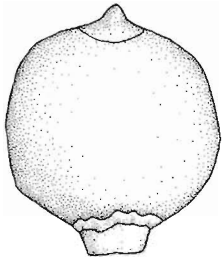
Astrocaryum jauari (Mart). – Jauarí, Arecaceae (Roosmalen 1985)

Fruit: one-seeded, yellow drupe; 4 x 2.5 cm
Seed: slightly smaller than the fruit; not floating; ichthyochorically dispersed (Piedade 1985)
Fructification: April to June
Relationship of pericarp to seed: 0.58 to 1 (w/w)
Water content: 40 %



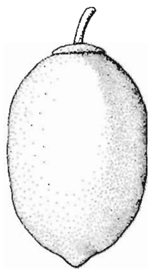
Euterpe oleracea – Assaí, Arecaceae (Roosmalen 1985)

Fruit: one-seeded, violet drupe; 1 x 1 cm; not floating; bird dispersal
Seed: slightly smaller than the fruit
Fructification: July to December
Water content: 37 %



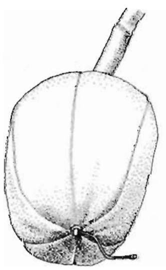
Pyrenoglyphis marajá (Mart. Burret) – Marajá, Arecaceae

Fruit: one-seeded, black-violet, more or less round drupe; 1cm
Seed: almost the same size as the fruit itself
Fructification: May
Water content: 61%



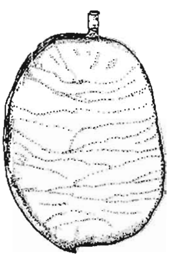
Crescentia amazonica (Ducke) – Cuia, Bignoniaceae

Fruit: many-seeded, green, hard berry; 7.5 x 4.5 cm; floating for 1–2 weeks; dispersal ichtyochorically (Ziburski 1990)
Seed: 0.75 x 0.45 cm
Fructification: over the whole year
Water content: 82%



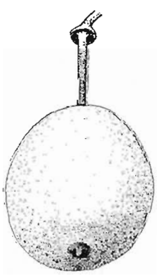
Pseudobombax munguba (Mart. & Zucc) Dugand – Munguba, Bombacaceae

Fruit: many-seeded, red capsule; 18 cm x 14 cm
Seed: oval, brownish-white striped; 0.3 mm x 0.2 mm
Fructification: July to October
Water content of the seeds: 35%



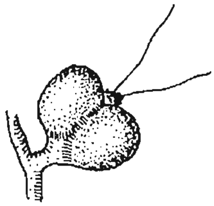
Macrolobium acaciifolium (Benth.) – Arapari, Caesalpinaceae (Roosmalen 1985)

Fruit: brown pod; 6 cm x 4.5 cm
Seed: one brown, flat, irregular four-sided seed, 4 cm x 2.7 cm
Fructification: February to June
Water content: 51%



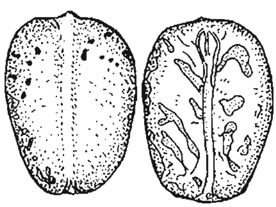
Crateva benthami (Eichl. in Mart.) – Catoré, Capparaceae

Fruit: many-seeded, pale green and white spotted, round berry; 5.7–11.5 cm diameter; the fruits ferment in the water and the developing gases make the fruits rise to the surface; dispersal ichtyochorically and hydrochorically
Seed: 1 x 0.8 cm
Fructification: January to August
Relationship of pericarp to seed: 0.78 to 1 (w/w)
Water content: 64%



Alchornea schomburgkiana – Supiarana, Euphorbiaceae (Roosmalen 1985)

Fruit: two- or three-seeded capsule; 1 x 0.7 cm
Seed: 0.6 x 0.4 cm; fruit was not separated for the analysis
Fructification: March, April
Water content: 75 %

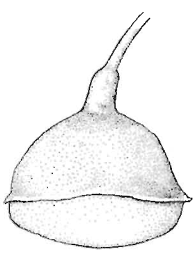


Hevea brasiliensis – Seringa verdadeira, Euphorbiaceae (Roosmalen 1985)

Fruit (not illustrated): brown, three-seeded capsule; 5 x 7 cm,
Seed (illustration): pale and dark brown; 2.3 x 1.2 cm; floating because of a tissue with large, air-filled lumen; dispersal hydrochorically
Fructification: March to July
Relationship testa to embryo (seed): 0.86 to 1 (w/w)
Water content of seeds: 14%

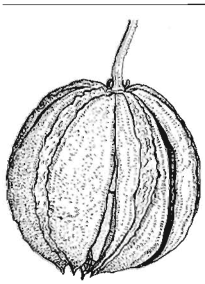
Nectandra amazonum (Nees.) – Loro, Lauraceae

Fruit: one-seeded, green berry; 2.5 x 1.5 cm; not floating; dispersal ichthyochorically by fishes living on the bed of the river (silurids) (Ziburski 1990).
Seed: slightly smaller than the fruit itself: the pericarp was not analyzed because of the difficulty of grinding it
Fructification: April to August
Water content: 78%



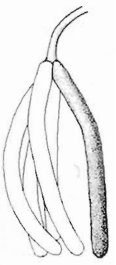
Eschweilera tenuifolia [(Berg) Miers] – Macacaricujá, Lecythidaceae

Fruit: many-seeded, woody, thin-walled pyx; 9 x 7 cm
Seed: angular, brown; 3.5 x 1.5 cm; floating maximally one day; dispersal hydrochorically
Fructification: February to April
Water content: 40%



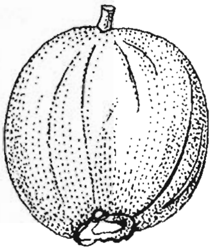
Carapa guianensis (Aubl.) – Andiroba, Meliaceae (Roosmalen 1985)

Fruit: many-seeded, brown capsule; 7.5 x 6.5 cm
Seed: 3.5 x 2.5 cm, 8 to 16 seeds per fruit
Fructification: July to December
Relationship pericarp to seed: 0.21 to 1 (w/w)
Water content: 60%



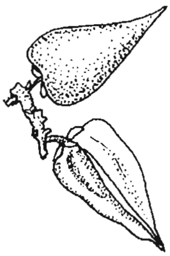
Cecropia latiloba (Miq.) – Embaúba, Moraceae

Fruit: greenish-brown multiple drupe; 16 x 1.5 cm, floating because of the air retained by the hair
Seed: 0.4 x 0.1 cm; one seed per fruit
Fructification: April to October
Water content: 74 %



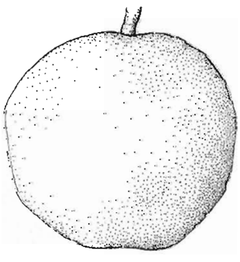
Psidium acutangulum. – Goiaba araçá, Myrtaceae (Roosmalen 1985)

Fruit: many-seeded, yellowish-green berry; 3 x 2.8 cm; floating because of fermentation gases; dispersal hydrochorically and endozoochorically
Seed: 0.8 x 0.6 cm
Fructification: March to July
Relationship pericarp to seed: 1.68 to 1 (w/w)
Water content: 73 %



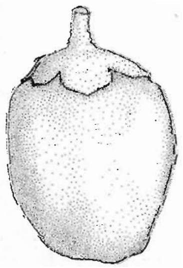
Symmeria paniculata (Benth.) – Caruaçú, Polygonaceae (Roosmalen 1985)

Fruit: three-sided, brown nut; 1.8 cm x 0.5 cm
Seed: one-seeded, the seed having almost the same size as the fruit
Fructification: March, April
Water content: 64 %



Pouteria glomerata (J.M.Pires & W.Rodriges) – Abiurana, Sapotaceae

Former name: *Neolobatia cuprea*
Fruit: one-to four-seeded, round berry; 5 cm; floating 7 to 29 days; dispersal hydrochorically and ichthyochorically (Ziburski 1990)
Fructification: February to August
Water content: 78 %



Vitex cymosa (Bert ex Spreng.) – Tarumã, Verbenaceae

Fruit: one-seeded, violet drupe; 2 cm x 1 cm
Seed: almost the same size as the fruit itself
Fructification: August, September
Water content: 88 %

Table 1 shows the chemical composition of all the fruit eaten by fish (according to the literature) and table 2 those that are probably also eaten but are not mentioned in the literature. They are ranked according to decreasing levels of crude protein. All fruit parts are listed together i.e. pericarp, seeds, testa and embryo. The chemical composition shows that seeds are, as expected, richer in crude protein and crude fat than the pericarp, which is itself richer in crude fibre. The fruit flesh is rich in soluble carbohydrates. The average for soluble carbohydrates is 67.3 % of dry mass, for crude fibre 29.6 %, for crude protein 6.5 %, for crude fat 18.9 % and for crude ash 5 % (from Table 1). Variation of contents in the different parts of the fruit is considerable. The average energy is 21.2 kJ/g dry matter and for phosphate 0.14 %, whereas without exception seeds have more phosphate and more calories than the pericarp.

The determination of polyphenols results only in relative values, which allow a comparison of the fruits with each other. The average is 6.1, whereas the seeds of *Hevea brasiliensis* and *Crateva benthami* with 2, and the seeds of *Astrocaryum jauari* with 2.7 have significantly lower levels. These three seeds are preferred

TABLE 1. Chemical composition of 19 fruit species eaten by fish in the inundated forests of Central Amazonia near Manaus

Species	crude protein % dry mass	crude fat % dry mass	crude fibre % dry mass	crude ash % dry mass	sol. carbohyd % dry mass	energy kJ/g d. mass	phosphate % dry mass	polyphenols (rel. values)	silicates % dry mass
Pseudobombax munguba	43.0	26.0	21.7	6.0	2.7	n.d.	n.d.	n.d.	0.32
Hevea brasiliensis embryo	23.8	44.3	3.9	4.0	24.1	32	0.26	n.d.	0.08
Hevea brasiliensis testa	3.0	0.6	66.6	1.0	28.7	n.d.	0.01	1.96	0.11
Cecropia latiloba	22.5	12.8	28.0	6.5	30.2	n.d.	n.d.	n.d.	0.37
Symmeria paniculata	20.4	1.3	24.5	2.5	51.3	n.d.	n.d.	n.d.	0.06
Macrolobium acaciifolium seed	20.3	1.4	11.7	1.5	65.1	n.d.	n.d.	n.d.	0.03
Macrolobium acaciifolium pericarp	9.7	1.6	42.0	2.5	44.2	n.d.	n.d.	n.d.	0.04
Crateva benthami seed	18.0	10.1	16.6	3.5	51.8	21	0.20	2.00	0.02
Crateva benthami pericarp	7.0	1.5	44.0	4.5	42.8	19	0.12	1.61	0.01
Alchornea schomburgkiana	17.4	9.9	2.2	5.0	65.5	23	0.18	10.00	n.d.
Crescentia amazonica seed	16.9	7.3	13.7	6.0	56.1	20	n.d.	3.36	0.15
Crescentia amazonica pericarp	7.3	1.5	36.5	3.0	51.7	n.d.	0.18	1.42	0.35
Vitex cymosa	12.5	2.2	38.0	5.0	42.3	n.d.	n.d.	n.d.	1.44
Annona montana seed	12.2	19.9	31.8	2.0	34.1	26	0.16	4.63	0.09
Annona montana pericarp	9.1	1.9	28.8	5.0	55.2	18	0.16	7.21	0.04
Nectandra amazonum seed	11.5	8.7	4.6	3.0	72.2	20	0.19	4.80	0.11
Eschweilera tenuifolia embryo	11.3	3.6	1.6	2.0	81.5	19	0.17	12.00	0.06
Eschweilera tenuifolia testa	9.6	1.0	11.9	1.0	76.6	n.d.	0.07	11.29	0.03
Eschweilera tenuifolia pericarp	7.7	1.8	9.7	1.0	79.9	18	0.02	n.d.	0.01
Astrocaryum jauari seed	10.9	33.3	17.5	1.0	37.2	25	0.18	2.71	0.12
Astrocaryum jauari pericarp	9.2	4.4	31.2	3.0	52.3	n.d.	0.11	6.79	0.49
Pouteria glomerata pericarp	9.9	6.0	13.3	4.5	66.3	18	0.11	10.02	0.04
Pouteria glomerata seed	8.0	3.5	27.3	2.5	58.7	20	0.05	n.d.	0.13
Carapa guianensis pericarp	9.5	1.1	16.3	5.0	68.1	n.d.	0.05	13.55	0.58
Carapa guianensis testa	7.8	8.2	36.2	1.0	46.7	n.d.	0.05	2.62	0.13
Carapa guianensis embryo	7.4	59.9	4.6	3.0	25.5	n.d.	0.12	5.88	1.14
Pyrenoglyphis maraja seed	9.3	24.9	6.5	2.0	57.3	24	1.40	1.30	0.01
Pyrenoglyphis maraja pericarp	7.0	1.1	17.9	3.0	71.1	n.d.	0.04	8.42	0.72
Euterpe oleraceae pericarp	8.1	15.3	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Euterpe oleraceae seed	7.2	2.5	8.1	1.0	81.2	n.d.	0.11	1.93	0.18
Psidium acutangulum seed	7.5	5.9	43.8	2.0	40.9	23	0.13	6.55	0.09
Psidium acutangulum pericarp	5.2	1.9	38.1	3.0	51.9	19	0.11	12.17	0.09
Ilex inundata	6.5	11.8	10.4	4.0	67.3	21	0.14	6.10	0.05

TABLE 2. Chemical composition of 11 fruit species from the inundated (*) and not inundated rainforest near Manaus

Species	crude protein % dry mass	crude fat % dry mass	crude fibre % dry mass	crude ash % dry mass	sol. carbohyd % dry mass	energy kJ/g d. mass	phos-phate % dry mass	poly-phenols (rel. values)	water content % fresh mass
Caesalpinia pulcherrima seed	20.2	5.5	14.3	2	57.9	19.1	0.20	11.88	63
Caesalpinia pulcherrima pericarp	4.4	1.4	45.1	2	47.1	n.d.	0.07	15.10	
Cariniana decandra seed	20.1	45.7	1.1	7	26.1	n.d.	10.62	n.d.	33
Cariniana decandra pericarp	2.9	0.5	39.8	2	54.8	n.d.	0.01	6.21	
Ipomoea species seed	19.0	6.0	26.7	3	45.3	n.d.	n.d.	n.d.	3
Ipomoea species pericarp	8.8	1.8	29.6	n.d.	n.d.	n.d.	1.80	n.d.	
Inga species*	16.3	1.8	13.4	4	64.5	18.3	0.14	n.d.	70
Aldina latifolia seed*	15.2	0.4	4.8	1	78.6	18.5	0.08	4.29	69
Aldina latifolia pericarp*	7.8	2.4	22.0	1	66.8	20.5	0.02	12.13	
Enterolobium species	12.8	1.9	30.4	3	51.9	19.4	0.14	10.08	16
Casearia species*	12.4	30.2	4.6	6	46.7	24.2	n.d.	4.87	62
Escleronema species seed	10.3	6.3	2.8	2	78.6	20.4	0.12	14.75	48
Escleronema species pericarp	6.6	1.7	22.8	3	66.0	n.d.	0.04	1.98	
Scleronema micranthum seed	8.8	11.5	2.6	2	75.1	23.2	0.08	10.13	37
Scleronema micranthum pericarp	7.3	1.6	26.7	3	61.4	20.3	0.04	n.d.	
*Phtirusa rufa**	8.6	18.1	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	66
Eugenia species	6.0	2.1	13.1	2	76.8	18.0	0.08	14.34	77

by fish, which allows the suggestion that fish have a low preference for bitter food. The silicate content has an average of 0.2 %.

Fruits with a high nutritional value are those with relatively high levels of crude protein and crude fat. The nutritional value of the seeds of such fruits is considerably higher than the corresponding pericarp or testa. Fruits with an average nutritional value have a smaller discrepancy between the contents of pericarp and seeds.

In this context, the water content of nutritionally rich fruits in comparison with other fruits must be questioned. The average water content of the examined fruits is 61 %. The individual water content ranges from a minimum of 14.6 % (*Hevea brasiliensis*) to a maximum of 88 % (*Vitex cymosa*). Fruits with high protein, fat and energy levels tend to have a water content which is far below the average, for example *Pseudobombax munguba* with a water content of 35 %. A contrary situation exists among fruits with a high water content, which normally have high levels of carbohydrates and relatively little protein and fat, for example *Psidium acutangulum* with a water content of 73 %. A comparative analysis could show that fruits eaten by humans belong mainly to the second group with high water content (comparisons taken from Souci *et al.* 1989, Waldhoff 1994).

Further detailed results from the 30 examined fruits are as follows:

1. Fruits separated for the analysis demonstrate in the majority of cases higher protein and fat contents in the seeds, and higher levels of soluble carbohydrates in the pericarp. Crude ash and crude fibre show no single tendency. Crude protein and crude fat are the critical nutrients in the chemical composition of a fruit, because they are the most important energy sources. Carbohydrates deliver comparatively less energy; they are immediately metabolized and not stored (Rehm & Espig 1976).
2. The energy content is higher in the seeds than in the pericarp. Golley (1961) tested 600 plants and concluded that coniferous seeds had the highest energy level at 23.5 kJ/g to 29.7 kJ/g. Of the plants of the inundated forest examined, *Hevea brasiliensis* seeds have the highest energy content (32.3 kJ/g), followed by *Annona montana* seeds (25.6 kJ/g), *Astrocaryum jauari* (24.8 kJ/g) and *Pyrenoglyphus maraja* (24.4 kJ/g). These seeds are among those with the highest energy levels known, surpassing the levels among conifers. All these seeds are preferred by fish.
3. The water content of fruits and seeds rich in crude protein and crude fat is normally less than fruits rich in soluble carbohydrates.

4. Nutritionally rich seeds (with a high level of protein and fat) normally have a nutritionally poor pericarp (high crude fibre level).
5. The phosphate content is higher in the seeds than in the pericarp. The average for measured phosphate concentration in fruits eaten by fish is 0.14 % dry matter, which conforms to the ranges determined by Allen (1974) of 0.05%–0.3%.
6. The polyphenol content is usually lower in the seeds than in the pericarp. This is to be expected considering the role of phenols (protection against animal consumption, Lodge 1991).
7. The crude ash content in fruits is generally low.
8. Seeds which are intact when excreted by fish are generally small; the corresponding pericarp has a higher nutrient level than the seeds, for example *Pouteria glomerata.*
9. Tests on the different floating capabilities are possible using scanning electron microscopy, as long as fresh material is available. *Annona montana* seeds have a single row of air-containing tissues, *Hevea brasiliensis* seeds have a series of rows with air-containing tissues, *Macrolobium acaciifolium* has a series of air-containing tissues in the fruit casing and *Cecropia latiloba* has many hairs which retain air and so enable them to float.

Fruit production. For all four species selected, fruit production is clearly during inundation phase (Fig. 1). For *P. glomerata* and *I. inundata,* berry dispersal starts with the onset of the high water season, while the berries of *P. acutangulum* fruit in the middle, and the drupes of *V. cymosa* towards the end of inundation.

Fruit dispersal (with 4–9 berries/m^2) of *P. glomerata* lasts over two months, with a peak after two weeks. This corresponds to a maximum mass of 447 g/m^2. The fruiting of *I. inundata* lasts over 13 weeks, starting slowly with an increase after 7 weeks. Maximum dispersal rate is 765 berries/m^2, corresponding to 157 g/m^2. Diaspores of *P. acutangulum* are released in the middle of June with a high number of 42 berries/m^2, corresponding to 475 g/m^2. There is almost a linear decrease in fruit dispersal which stops after four weeks. The last species investigated was *V. cymosa.* In this five-week trial there was only a small variation in the dispersal rate between 113 and 159 drupes/m^2. This corresponds to 205–323 g/m^2.

Stomach content. The results of a comparative study lasting two years, on the impact of the inundated forest on fishes of a black and a white water area,

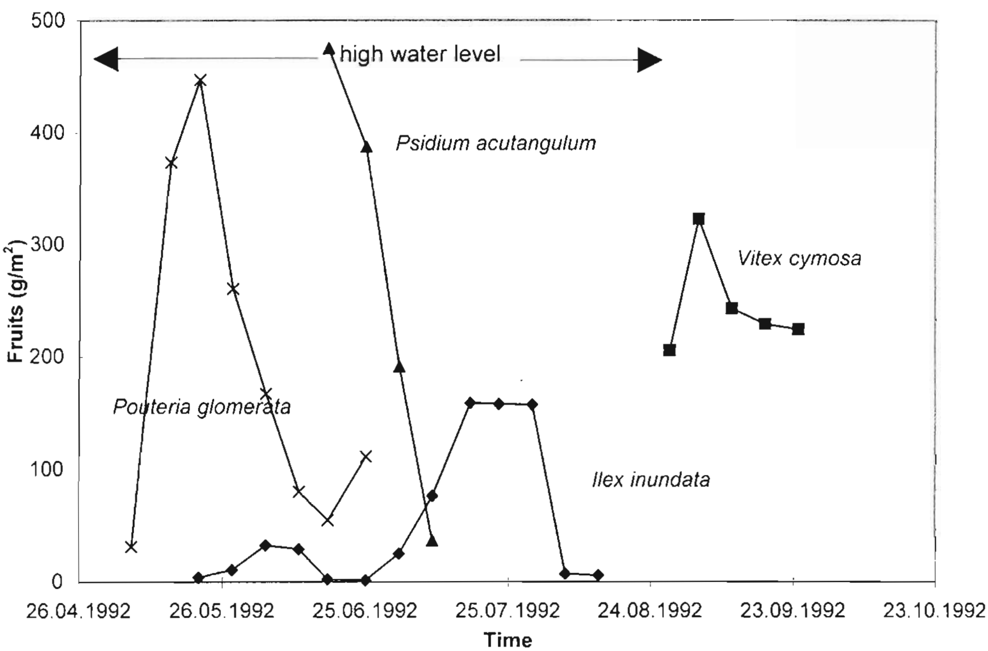


FIG. 1. Fruit production of 4 species during inundation phase

TABLE 3. Occurrence of food items in the stomach of fish from black water and white water

Food item	rising black	rising white	high black	high white	falling black	falling white	low black	low white
Fruits/seeds	31	18	40	24	36	54	38	48
Allochtonous arthropods	15	24	45	22	50	53	54	44
Aquatic insect larvae	12	16	18	16	3	10	11	2
Crustacea/Molluscs	18	11	5	–	31	10	17	36
Fish	37	3	31	9	19	31	45	83
Zooplankton	–	16	–	2	1	34	1	4
Algae/Macrophytes	–	1	41	–	0	2	21	3
Detritus	41	39	55	46	67	60	41	65

reveal that 23 species from the white water and 34 species from the black water feed on fruits, corresponding to 22 % and 13 % respectively of the total species number captured in the area (Tab. 3). As a more quantitative investigation on nutritional biology could not be carried out under field conditions, data given refer to the frequency of occurrence as an estimate of the proportion of the population that feeds on the particular food item. However, predatory species are not considered.

Furthermore, the analysis of seasonal variations reveals that black water species feed more constantly on food from the floodplain forest than white water species, probably due to the high diversity of food items in the várzea. Ranking the food occurrence within a season, fruits are higher ranked in white than in black water. In black water the ranking of occurrence at rising, high, falling and low water is 3, 3, 3, 4 and in white water 3, 2, 2, and 3 respectively. The frequency of occurrence in the black water fish for fruits and seeds is between 31 % and 40 %. In the white water, fruit-feeding increases from 18 % at rising water to 54 % at falling water level. The value decreases at low water level to 48 %.

Comparing stomach contents of fishes from black water and white water, most Rio Negro fishes appear to be omnivorous on a seasonal basis, with fruits, allochthonous arthropods, crustaceans, fish and detritus as the most important food items, while in white water, in addition, zooplankton, and in black water, algae become major food categories. Predation is of importance for black water fish during rising and high water, and for white water fish during falling and low water level. Zooplankton is of seasonal importance only in white water, while in black water, fish feed during certain periods of the year on algae. In both sample sites there were no fishes feeding on macrophytes. Of interest is that forest plant material is available and consumed by fish over the whole year and not only when the forests are flooded, as is demonstrated by stomach contents during low and rising water level.

DISCUSSION

Floodplains, with floodplain forests, floating meadows and algae/zooplankton communities as their three main food sources, contain the most productive habitats of the Amazon river system. The relative importance of each habitat component is not very clear. We know that fruit- and seed-eating fish species constitute a major share of the annual catch. Additionally we know that many omnivorous fish occasionally feed on fruits and seeds too. This is why fish biodiversity depends to a large extent on an undisturbed floodplain and that deforestation endangers many fish species, some of which are even of high commercial value.

The fish ecological studies were carried out in two specific areas of the várzea and the black water. It was shown that 23 fish species from the white and 34 from the black water had fruits and seeds in their stomach contents. As the total number of species identified in both areas represents less that 10 % of the whole ichthyofauna of Amazonia, the total number of frugivorous species must be significantly higher. Literature data reveal an estimate of 200 fish species in Amazonia that feed on fruits and seeds (Gottsberger 1978; Goulding 1980; Kubitzki 1985, 1989; Ziburski 1991; Kubitzki & Ziburski 1994).

Apart from Waldhoff (1991, 1994), relatively few authors have examined the nutrient composition of fruits and seeds from floodplain forests. Aguiar *et al.* (1980) analyzed Amazonian fruits consumed by humans. Göhl's (1981) chemical analysis of tropical fruits, including *Hevea brasiliensis*, achieved results similar to those obtained in this study. The crude fat content in both studies is 45 %, the crude ash content 3 %, the crude fibre content 4 %. The crude protein levels found in this study are somewhat higher, the levels of soluble carbohydrates somewhat lower. Almeida & Valsechi (1966) analyzed the chemical content of a number of fruits, including many Amazonian species. However the results differ from those presented here, possibly because the seeds originated from southern Brazil (São Paulo). Balick (1979) examined oil-producing palms from the Amazon area, establishing an oil content for *Astrocaryum jauari* of 36 %, which corresponds to results obtained in this study.

The nutritional value of those fruits from the floodplain forests used as fish fodder depends on their chemical composition. For comparison, some arbitrarily chosen fruit of world-wide commercial value were analyzed in the same manner as the others: *Actinidia chinesis* (kiwi), *Musa paradisiaca* (banana) and *Prunus persica* (peach). These fruits show a real different chemical composition from those eaten by fish. The commercial fruit are normally fleshy and juicy, with high water (81 %) and soluble carbohydrate (72 %) levels which deliver the sweet and the juicy consistence. Nuts were not included in our considerations because at our sampling sites nuts are scarce, except those of *Symmeria paniculata*, which, however, have a very small seed. The two properties, sweet and juicy, are remarkable for fruits eaten by humans. By contrast, most of the fruits eaten by fish do not have such a high water and soluble carbohydrate content, but higher fat and protein content, so that the caloric value and delivered energy is considerably higher and more important than the taste. We could say that the different function of fruit as food source for man and fish is clear: for man fruits are mostly complementary to the main meal, while for some fishes the fruits are the main meal and almost the only energy source.

There are some data on seasonal changes of body composition with regard to frugivorous feeding habits (Saint-Paul 1984, Junk 1985, Kohla *et al.* 1992). However, there is little information on the effect of differing nutritional composition of fruits and seeds on growth rate and body composition. In a feeding experiment with the Serrasalmid fish *Colossoma macropomum*, using different fruits from the floodplain forest (*P. munguba*, *Hevea* sp., *C. latiloba*), growth rates were correlated with the protein content of the food source. The best growth rate obtained was 1.3 % /day when feeding *P. munguba* (Roubach & Saint-Paul 1994). In another trial, which was carried out to study protein requirement and the efficiency of metabolizable vegetable protein, the highest weight increase (1.64 %/day), and the lowest feeding rate, was obtained with a 50 % crude protein fishmeal-free diet (Kohla *et al.* 1992). There is little other information on growth rate of Neotropical fish when feeding on vegetable material. In a more recent investigation, nutrients, energy and apparent digestability of fruits and seeds consumed by *C. macropomum* have been studied showing good results with these food items (Silva 1996). Stomach contents of wild fish and feeding experiments indicate that fishes increase their weight when using food sources of the floodplain forest. A total number of 30 different fruits were identified as being consumed by fish. However, the realistic estimate might increase when more areas have been studied. There is still no information on how many trees of the floodplain forest really produce edible fruits. Phytosociological studies on composition and structure of white water floodplain forests revealed a figure of 500 trees/ha (Balslev *et al.* 1987, Foster 1990, Campbell *et al.* 1992).

As the total area of floodplain forests is estimated to be 70 000 km^2, this means a total tree number of 3.5 billion in Amazonia with the potential to sustain fish populations. Assuming that only 25 % of this number or area is of importance for fish, there are approximately 875 million trees which produce important fish food every year during high water. In the present, study fruit production/m^2 of the four species varied between approximately 150 and 500 g/m^2 and week. Assuming an average fruiting period of 6 weeks, an annual production between 9 and 30 t/ha can be expected. If the fraction of floodplain forest important for fish is really 25 %, the total annual production of the whole floodplain forest can be estimated to be between 16 and 53 million tons of fruits. If only 10 % of this production is consumed by fish, and assuming a conversion factor of 1:10, which is realistic for this type of vegetal material, the fruit output corresponds to a fish production of between 160 000 and 530 000 t/year. Considering a mean fish price of US$ 0.5–1.0/kg in Amazonia (Petrere 1992), the monetary value of the fish production from the floodplains can be estimated to be in the range of US $ 320 to 530 million per year.

Many Amazonian fish depend on the floodplain forest for feeding and protection. Some of the most important species, e.g., *Colossoma macropomum*, feed only in the floodplain forest, while they starve in the main river channel during low water. The monetary estimation shows clearly the economic importance of the floodplain forest for fishery. However, vast areas of floodplain forest have already been massively deforested during the last three decades for agricultural purposes or cattle raising. This not only endangers the biodiversity of the Amazonian ichthyofauna but might also have negative implications for fish landings. Even if we do not know the minimum size of floodplain forest necessary to sustain fish populations, the dependence of many commercial fish species on floodplain forests, and the high economic value of their fish production, are powerful arguments for the protection of this habitat.

The problems of overfishing in the region of Manaus, the region's high population growth, and the natural variation in fish catches (corresponding to large catches in low water periods and smaller catches in high water periods) lead to shortages in the fish supply (Saint Paul 1982). Local fish-farming presents a possibility of overcoming shortages in the fish supply and of maintaining low fish prices. Concerning the planning of larger-scale fish farming, fruit types which are already consumed by fish could be used as a feed source. The use of such fruits species that have a high nutritional value and do not only grow in the flooded forest but also in the non-flooded forest could be recommended. In this case collection of fruits is much easier. Examples are the fruits *Hevea brasiliensis* and *Carapa guianensis*, both of which contain extremely high levels of crude fat and sufficient levels of crude protein, and are abundant species not only in the floodplains but also in the non flooded forests, the so-called terra firme.

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REFERENCES

Aguiar, J.P.L., Marinho, H.A., Rebelo, Y.S., & R. Shrimpton. 1980. Aspectos nutritivos de alguns frutos da Amazônia. Acta Amazônica 10: 755–758.

Allen, S.E. 1974. Chemical analysis of ecological material. Oxford.

Almeida, J.R., & O. Valsechi. 1966. Guia de composição de frutas. Instituto Zimotécnico da Escola Superior de Agricultura Luiz de Queiroz da USP, Piracicaba.

Anonymus. 1969. Méthodes de référence pour la détermination des éléments minéraux – dans les végetaux (Azète, phosphore, potássium, sodium, calcium, magnesium). Agronomie tropical, Série II, 24: 827–835.

Balick, M.J. 1979. Amazonian oil palms of promise: a survey. Economic Botany 33: 11–28.

Balslev, H., Luteyn, J., & B. Ollgaard. 1987. Composition and structure of adjusted unflooded and floodplain forest in Amazonian Ecuador. Opera Botanica 92: 37–57.

Boberfeld, W.O. von. 1994. Grünlandlehre, biologische und ökologische Grundlagen. Stuttgart.

Campbell, D.G., Stone, J.L., & A.Jr. Rosas. 1992. A comparision of the phytosociology and dynamics of three floodplain (várzea) forests of known age, Rio Juruá, western Brazilian Amazon. Bot. J. Linn. Society 108: 213–237.

Colonnello, G. 1991. Phenological observations and forest litter production in a flooded forest (várzea) of the Orinoco River, Venezuela. Interciência 16: 202–208.

Foster, R. 1990. The floristic composition of the Rio Manú floodplain forest. Four Neotropical rainforests. New Haven.

Furch, K. 1984. Water chemistry of the Amazon basin: The distribution of chemicals elements among freshwaters. Pp. 189-204 *in* Sioli, H. (ed.). The Amazon, Limnology and landscape ecology of a mighty tropical river and its basin. Dodrecht.

Göhl, B. 1981. Tropical feeds, feed information summaries and nutritive values. Rome.

Golley, F.B. 1961. Energy values of ecological materials. AEC, Savannah River Project, University of Georgia. Ecology, 42: 581–584.

Gottsberger, G. 1978. Seed dispersal by fish in the inundated regions of Humaitá, Amazonia. Biotropica 10: 170–183.

Goulding, M. 1980. The fishes and the forest: explorations in Amazonian natural history. Berkely.

Goulding, M. 1983. The role of fishes in seed dispersal and plant distribution in Amazonian floodplains ecosystems. Sonderb. naturwiss. Ver. Hamburg 7: 271–283.

Goulding, M. 1985. Forest fishes of the Amazon. Pp. 267–276 *in* Prance, G.T, & T.E. Lovejoy (eds.). Key enviroments Amazonia. New York.

Goulding, M. 1989. The flooded forest. London.

Goulding, M., Carvalho, M.L., & E.G.Ferreira. 1988. Rio Negro, rich life in poor water. Hague.

Goulding, M., Smith, N.J.H., & D.J. Maghar. 1996. Flood of fortune. Ecology and economy along the Amazon. New York.

Honda, E.M.S. 1974. Contribuição ao conhecimento da biologia de peixes do Amazonas, II- Alimentação do tambaqui, Colossoma bidens. Acta Amazônica 4: 47–53.

Junk, W.J. 1985: Temporary fat storage, an adaptation of some fish species to the waterlevel fluctuations and related environmental changes of the Amazon river. Amazoniana 9: 315–351.

Kling, H.G.C., & G.W. Heath. 1967: The chemical analysis of small samples of leaf material and the relationship between disappearence and composition of leaves. Pedobiologia 7: 192–197.

Kohla, U., Saint-Paul, U., Friebe, J., Wernicke, D., Hilge, V., Braum, E., & J. Gropp. 1992. Growth, digestive enzyme activities and hepatic glyogen levels in juvenile *Colossoma macropomum* Cuvier from South America during feeding, starvation and refeeding. Aquacult. Fish. Manage. 23: 189–208.

Kubitzki, K. 1985. Ichthyochory in *Gnetum venosum*. An. Acad. Brasil. Cienc. 57: 513–516.

Kubizrki, K. 1989. The ecogeographical differentation of Amazonian inundated forests. Plant Systematics and Evolution 162: 285–304.

Kubitzki, K., & A. Ziburski. 1994. Seed dispersal in flood plain forests of Amazonia. Biotropica 26: 30–43.

Lodge, D.M. 1991. Herbivory on freshwater macrophytes. Aquatic Botany 41: 195–224.

Naumann, C., Bassler, R., Seibold, R., & C. Barth. 1976. Verband Deutscher Landwirtschaftlicher Untersuchungs- und Forschungsanstalten; Methodenbuch Band III; die chemische Untersuchung von Futtermitteln. Darmstadt.

Petrere Jr., M. 1992. Pesca na Amazônia. Simdamazônia. Seminário Internacional sobre Meio Ambiente, Pobreza e Desenvolvimento da Amazônia. (Editors) SECTMA and Governo do Estado do Pará PRODEPA, Belém.

Piedade, M.T.F. 1985. Ecologia e biologia reproductiva de *Astrocaryum jauari* Mart. (Palmae) como exemplo de população adaptada as áreas inundáveis do Rio Negro (igapós). Tese de mestrado, INPA/FUA, Manaus.

Pires, J.M. 1972. Tipos de vegetação da Amazônia. Mus. Paraense E. Goeldi 20: 179–202.

Rehm, S., & G. Espig. 1976. Die Kulturpflanzen der Tropen und Subtropen. Stuttgart.

Revilla, J. 1991. Aspectos florísticos e estruturais da floresta inundável (Várzea) do Baixo Solimões, Amazonas, Brasil. Tese de doutorado, INPA, FUA. Manaus.

Roosmalen, M.G.M. van. 1985. Fruits of the Guianian flora. Wageningen.

Roubach, R. 1991. Uso de frutos e sementes de florestas inundáveis na alimentação de *Colossoma macropomum*. Tese de mestrado, INPA, FUA. Manaus.

Roubach, R., & U. Saint-Paul. 1994. Use of fruits and seeds from Amazonian inundated forests in feeding trials with *Colossoma macropomum* (Cuvier, 1818) (Pisces, Characidae). J. Appl. Ichthyol.10: 134-140.

Saint-Paul, U. 1982. Ökologische und Physiologische Untersuchungen an dem Amazonasfisch Tambaqui (*Colossoma macropomum*) im Hinblick auf seine Eignung für die tropische Fischzucht. Dissertation zur Erlangung des Doktorgrades des Fachbereiches Biologie der Universität Hamburg.

Saint-Paul, U. 1984. Investigations on the seasonal changes in the chemical composition of liver and condition from a Neotropical characoid fish *Colossoma macropomum* (Serrasalmidae). Amazoniana 9: 147–158.

Silva, M.F., Lisbôa, P.L.B., & R.C.L. Lisbôa. 1977. Nomes vulgares de plantas amazônicas. Manaus.

Silva, J.A. Moreira da. 1996. Nutrientes, energia e digestibilidade aparente de frutos e sementes consumidos pelo tambaqui (*Colossoma macropomum* Cuvier) nas florestas inundáveis da Amazônia Central. Tese de doutorado, INPA, UFAM. Manaus.

Smith, N.J.H. 1979. A pesca no rio Amazonas. Manaus.

Souci, S.W., Fachmann, W, & H. Kraut. 1989. Die Zusammensetzung der Lebensmittel, Nährwert-Tabellen 1989/1990. Stuttgart.

Waldhoff, D. 1991. Morphologie, Nährwert und Bioelementgehalte hydrochor und zoochor verbreiteter Früchte und Samen aus amazonischen Überschwemmungswäldern bei Manaus. Diplomarbeit, Universität Kiel.

Waldhoff, D. 1994. Analyse von Früchten aus den Überschwemmungswäldern Zentralamazoniens und dem Pantanal Matogrossense in Hinsicht auf ihren Wert als Nahrung für kommerziell zu nutzende Fischarten. Dissertationsarbeit, Universität Kiel.

Ziburski, A. 1990. Ausbreitungs- und Reproduktionsbiologie einiger Baumarten der amazonischen Überschwemmungswälder. Promotionsarbeit, Hamburg.

Ziburski, A. 1991. Dissimination, Keimung und Etablierung einiger Baumarten der Überschwemmungswälder Amazoniens. Tropische und Subtropische Pflanzenwelt 77: 1–96.