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

Danielle Waldhoff*, Ulrich Saint-Paul1 & Bodo Furch2

1 Botanisches Institut der Universität Kiel, Olshausenstr. 40, D-24098 Kiel, Germany (Corresponding authors) 
2 Zentrum für Marine Truppenökologie, Fahrenheitstr. 1, D-28359 Bremen, Germany

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-sheding 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 biotopes, 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, Colonello 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 Colosoma 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). Colosoma 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 benjami. Sinking fruits are also eaten, e.g., by ground dwelling fish like Lithodoma 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, Baisley 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 javari produces 1.7 t of fruit per year and hectare, Pseudobombax manguba 2.2 t and Crateva benjami 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
of some tree species to ichthyochorous propagation; Pinede (1983) and Kubitzki (1983) 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 610 000 t 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:

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Annona montana</em></td>
<td>Graviola</td>
<td>Annonaceae</td>
</tr>
<tr>
<td><em>Ilex inundata</em></td>
<td>Mongulu</td>
<td>Aquifoliaceae</td>
</tr>
<tr>
<td><em>Astrocaryum jauari</em></td>
<td>Jauari</td>
<td>Areceae</td>
</tr>
<tr>
<td><em>Euterpe oleracea</em></td>
<td>Assai</td>
<td>Areceae</td>
</tr>
<tr>
<td><em>Pyrenophyta maraja</em></td>
<td>Maraja</td>
<td>Areceae</td>
</tr>
<tr>
<td><em>Crescentia amazonica</em></td>
<td>Cuia</td>
<td>Areceae</td>
</tr>
<tr>
<td><em>Pseudobombyx monguba</em></td>
<td>Monguba</td>
<td>Bignoniaceae</td>
</tr>
<tr>
<td><em>Macrolobium acaciifolium</em></td>
<td>Anapari</td>
<td>Bombaceae</td>
</tr>
<tr>
<td>* Crateva benthami*</td>
<td>Catoré</td>
<td>Caesalpinaceae</td>
</tr>
<tr>
<td><em>Alchornea schomburgkiana</em></td>
<td>Supianama</td>
<td>Capparaceae</td>
</tr>
<tr>
<td><em>Huea brasiliensis</em></td>
<td>Seringa verdadeira</td>
<td>Euphorbiaceae</td>
</tr>
<tr>
<td><em>Nectandra amazonum</em></td>
<td>Loro</td>
<td>Euphorbiaceae</td>
</tr>
<tr>
<td><em>Eschweileria tenuifolia</em></td>
<td>Mazacaricajá</td>
<td>Lauraceae</td>
</tr>
<tr>
<td><em>Canu guianensis</em></td>
<td>Andiroba</td>
<td>Lecythidaceae</td>
</tr>
<tr>
<td><em>Cecropia latiloba</em></td>
<td>Embauba</td>
<td>Meliaceae</td>
</tr>
<tr>
<td><em>Psidium acutangulum</em></td>
<td>Giaiba açaí</td>
<td>Moraceae</td>
</tr>
<tr>
<td><em>Symmeria paniculata</em></td>
<td>Curauá</td>
<td>Myrtaceae</td>
</tr>
<tr>
<td><em>Pouteria glomerata</em></td>
<td>Abiuana</td>
<td>Polygonaceae</td>
</tr>
<tr>
<td><em>Vitex cymosa</em></td>
<td>Tarumá</td>
<td>Sapotaceae</td>
</tr>
</tbody>
</table>

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:

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Esceronema species</em></td>
<td>Campinarana</td>
<td>Bombacaceae</td>
</tr>
<tr>
<td><em>Scleromom micrantum</em></td>
<td>Cardeiro</td>
<td>Bombacaceae</td>
</tr>
<tr>
<td><em>Aelda latifolia</em></td>
<td>Macauí do Igapó</td>
<td>Caesalpinaceae</td>
</tr>
<tr>
<td><em>Caesalpinia pulcherrima</em></td>
<td>Breu-de-estudante</td>
<td>Caesalpinaceae</td>
</tr>
<tr>
<td><em>Ipomoea species</em></td>
<td>unknown</td>
<td>Convovulaceae</td>
</tr>
<tr>
<td><em>Casuaria species</em></td>
<td>Sardineira vulgar</td>
<td>Flacourtiacae</td>
</tr>
<tr>
<td><em>Carnicina decandra</em></td>
<td>Tatuari</td>
<td>Lecythidaceae</td>
</tr>
<tr>
<td><em>Phytiria rufa</em></td>
<td>Erva-de-pasarinho</td>
<td>Lorantheaceae</td>
</tr>
<tr>
<td><em>Enterolobium schomburgkii</em></td>
<td>Orelha-de-macaco</td>
<td>Mimosaceae</td>
</tr>
<tr>
<td><em>Inga species</em></td>
<td>Ingá</td>
<td>Mimosaceae</td>
</tr>
<tr>
<td><em>Eugenia cumini</em></td>
<td>Ascitona</td>
<td>Myrtaceae</td>
</tr>
</tbody>
</table>
Sampling site. The fruits were collected from three
different locations in the surroundings of Manaus,
in Central Amazonia: a white water forest (\textit{várzea})
on the island of Ilha da Marchantaria (59°58'W, 3°2'S) in the river Solimões, in a black water forest
(\textit{iapã}) 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 nutrients 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 tree
species (\textit{Vitex cymosa, Psidium acutangulum, Illex
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\textsuperscript{3} 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

Fruit chemical composition. A classical Weender Anal-
ysis, 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 \textit{et al.} 1976). This is in accordance with
internationally recognized proximate analysis, which

is still in wide use and which allows easy compar-
isons, e.g., Boberfeld (1994). Polyphosphates (Ano-
nymus 1960) 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 Manacapuru). 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 investi-
gation.

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:
fish/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 commu-
nity, the occurrence of each food item within the
community was calculated in percentage.

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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 endozoochonically 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). – Jauari, 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* – Assai, 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 maraja** (Mart. Burret) – Maraja, Arecaceae

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

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**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%

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**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%

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**Macrololobium 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%

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**Crataeva 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 ichthyochorically 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 %

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*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%

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*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 (silurida) (Zbiralski 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%

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*Eschweilera tenusfolia* [(Berg) Miers] – Macacariçá, 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%

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*Canapa 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, Myrtraceae (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.) – Caruacú, 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) – Aburián, 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 0.1, whereas the seeds of *Hevea brasiliensis* and *Crataeva benthami* with 2, and the seeds of *Astrocaryum jauari* with 2.7 have significantly lower levels. These three seeds are preferred.

<table>
<thead>
<tr>
<th>TABLE 1. Chemical composition of 19 fruit species eaten by fish in the inundated forests of Central Amazonia near Manaus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
</tr>
<tr>
<td>----------------------------------------------</td>
</tr>
<tr>
<td><em>Pseudobombax munguba</em></td>
</tr>
<tr>
<td><em>Hevea brasiliensis</em> embryo</td>
</tr>
<tr>
<td><em>Hevea brasiliensis</em> testa</td>
</tr>
<tr>
<td><em>Crecopia latifolia</em></td>
</tr>
<tr>
<td><em>Symmeria paniculata</em></td>
</tr>
<tr>
<td><em>Macrolobium acaudifolium</em> seed</td>
</tr>
<tr>
<td><em>Macrolobium acaudifolium</em> pericarp</td>
</tr>
<tr>
<td><em>Crataeva benthami</em> seed</td>
</tr>
<tr>
<td><em>Crataeva benthami</em> pericarp</td>
</tr>
<tr>
<td><em>Alchornsea schoenburgiana</em></td>
</tr>
<tr>
<td><em>Cresciatia amazonica</em> seed</td>
</tr>
<tr>
<td><em>Cresciatia amazonica</em> pericarp</td>
</tr>
<tr>
<td><em>Vitex cyanos</em></td>
</tr>
<tr>
<td><em>Annona montana</em> seed</td>
</tr>
<tr>
<td><em>Annona montana</em> pericarp</td>
</tr>
<tr>
<td><em>Nectandra amazonum</em> seed</td>
</tr>
<tr>
<td><em>Eschweileria tenufolia</em> embryo</td>
</tr>
<tr>
<td><em>Eschweileria tenufolia</em> testa</td>
</tr>
<tr>
<td><em>Eschweileria tenufolia</em> pericarp</td>
</tr>
<tr>
<td><em>Astrocaryum jauari</em> seed</td>
</tr>
<tr>
<td><em>Astrocaryum jauari</em> pericarp</td>
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<tr>
<td><em>Pouteria glomerata</em> pericarp</td>
</tr>
<tr>
<td><em>Pouteria glomerata</em> seed</td>
</tr>
<tr>
<td><em>Carapa guianensis</em> seed</td>
</tr>
<tr>
<td><em>Carapa guianensis</em> testa</td>
</tr>
<tr>
<td><em>Carapa guianensis</em> embryo</td>
</tr>
<tr>
<td><em>Pyrenoglyphis manuza</em> seed</td>
</tr>
<tr>
<td><em>Pyrenoglyphis manuza</em> pericarp</td>
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<tr>
<td><em>Euterpe oleracea</em> seed</td>
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<tr>
<td><em>Psidium acutangulum</em> seed</td>
</tr>
<tr>
<td><em>Psidium acutangulum</em> pericarp</td>
</tr>
<tr>
<td><em>Ixora inundata</em></td>
</tr>
</tbody>
</table>
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 75%. 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 Pyrenogyphus 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/m²) of *P. glomerata* lasts over two months, with a peak after two weeks. This corresponds to a maximum mass of 447 g/m². The fruiting of *I. inundata* lasts over 13 weeks, starting slowly with an increase after 7 weeks. Maximum dispersal rate is 765 berries/m², corresponding to 157 g/m². Diaspores of *P. acutangulum* are released in the middle of June with a high number of 42 berries/m², corresponding to 475 g/m². 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/m². This corresponds to 205–325 g/m².

**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,
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 chinensis* (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 *Colosoma 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 digestibility 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 km², 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/m² of the four species varied between approximately 150 and 500 g/m² and week. Assuming an average fruiter 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.
VALUE OF FRUITS AND SEEDS

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 Hetera 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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