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The role of periphytic N_2 fixation for stands of macrophytes in the whitewater floodplain (várzea)*

by

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Abstract

In the várzea of Amazon River on Marchantaria Island, N_2 fixation was measured in the root-periphyton complex of three abundant macrophytes, i.e. *Paspalum repens*, *Echinochloa polystachya* and *Eichhornia crassipes*. The short-term study was set at a period of rising water when the biomass production of macrophytes is high. N_2 fixation was low in a main channel that links the river to the lakes, and it was high in Lakes Camaleão and Novo, the latter being a newly formed lake in the young sedimentation area of Marchantaria Island. The main factor controlling N_2 fixation on Marchantaria Island seemed to be O_2. The highest nitrogen input by N_2 fixation was observed in stands of *Paspalum repens* followed by *Echinochloa polystachya* and *Eichhornia crassipes*. Maximum rate of N_2 fixation reached 821.3 nmol N g DW^{-1} h^{-1} in the root-periphyton complex of *Paspalum repens* at Lake Camaleão. Under dark conditions there was always a decline in the rate of N_2 fixation pointing to the predominance of photoautotrophic cyanobacteria. Considering both N_2 fixation in the light and in the dark, related to the biomass of each macrophyte stand, N input in all three macrophyte stands was highest at Lake Novo. Upscaling the rates of N_2 fixation, the input at Lake Novo was 235 kg N ha^{-1} yr^{-1}, 37 kg N ha^{-1} yr^{-1} and 1 kg N ha^{-1} yr^{-1} in the stands of *Paspalum*, *Echinochloa* and *Eichhornia*, respectively. It is concluded that *Paspalum* and its N_2 fixing periphyton has a fertilizing potential that plays an important role for autogenic succession in the várzea.

Keywords: **Nitrogen turnover, N_2 fixation, periphyton, *Paspalum*, floodplain, Amazonia.**

Resumo

A fixação de N_2 foi medida no complexo perifiton-raízes de três macrófitas aquáticas abundantes (*Paspalum repens*, *Echinochloa polystachya* e *Eichhornia crassipes*) em lagos de várzea da Ilha de Marchantaria localizada no Rio Solimões/Amazonas, perto de Manaus. O estudo foi realizado no começo da enchente quando a produção de biomassa de macrófitas é alta. A fixação de N_2 foi baixa no canal principal de conexão do rio aos lagos no interior da ilha e alta no Lago Camaleão e no Lago Novo, um lago recém formado na área de sedimentação da Ilha de Marchantaria. O principal fator controlando a fixação de N_2 nos lagos da ilha aparenta foi o O_2. A principal entrada de N originou-se da fixação de N_2 observada no complexo perifiton-raízes de *Paspalum repens*, seguida das taxas observadas no complexo

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perifiton-raízes de *Echinochloa polystachya* e *Eichhornia crassipes*. A taxa máxima de fixação de N_2, 821,3 nmol N g $PS^{-1} \cdot h^{-1}$, ocorreu no complexo perifiton-raízes de *Paspalum repens* no Lago Camaleão. No escuro sempre houve diminuição na taxa de fixação de N_2, o que sugere predominância de cianobactérias fotoautotróficas. Levando em conta as taxas de fixação de N_2, tanto na luz quanto no escuro, e também a biomassa das macrófitas, observa-se que a entrada de N foi maior no Lago Novo. Em termos de área a entrada de N no lago Novo foi calculada em 235 kg N $ha^{-1} \cdot a^{-1}$, 37 kg N $ha^{-1} \cdot a^{-1}$ e 1 kg N $ha^{-1} \cdot a^{-1}$ no complexo perifiton-raízes de *Paspalum repens*, *Echinochloa polystachea* e *Eichhornia crassipes*, respectivamente. Em conclusão, *Paspalum repens* e a fixação de N_2 pelo perifiton associado às suas raízes exercem um importante papel na fertilização e na sucessão autogênica da várzea.

Introduction

The Amazon River drains the largest watershed in South America, and includes upland forests and lowlands covered by inundation forests and extensive macrophyte stands. Due to oscillations of the water level there is a shift between aquatic and terrestrial environments within the Amazon floodplain (várzea). Primarily, the low lying areas on Marchantaria Island ranging between 17 and 22 m above sea level (a.s.l.) are suitable habitats for highly productive aquatic and semi-aquatic macrophytes. Despite water level fluctuations of more than 10 m, macrophytes have developed strategies to form large stands in this environment, which shows a rapid turnover of nutrients (JUNK 1970; PIEDADE et al. 1997).

Ammonium (NH_4^+) and nitrate (NO_3^-) are the major nitrogen compounds available for microbial conversion and plant uptake. In the river channel NO_3^- is the predominant dissolved N compound, in the floodplain lakes NH_4^+ occurs at high concentrations as shown for Lake Camaleão (FURCH 1999). These diverse hydrochemical properties are due to a varied oxygen supply in the river and the várzea, which results in a different nitrification rate. This means that the intensity of nitrification is linked with other oxygen producing and consuming processes such as the decomposition of organic material, which occurs at high rates within the várzea (PIEDADE et al. 1991; FURCH & JUNK 1992; DARWICH 1995; DARWICH et al. 2000).

Although the river water is rich in major solutes, the N requirement for the net primary production of herbaceous vegetation of up to 100 t ha^{-1} yr^{-1} is not met by the input of river water (KERN & DARWICH 1997). Therefore, other N sources have to be taken into account. One example is the utilization of atmospheric N_2 by N_2 fixation which has already been described for the várzea by SALATI et al. (1982), MELACK & FISHER (1988), MARTINELLI et al. (1992), DOYLE & FISHER (1994) and KERN (1995). In this context the root-periphyton complex of aquatic macrophytes plays an important role in the gaseous N turnover. Besides the floodplain forest where KREIBICH (2002) recently found a high N input by N_2 fixation, it is suggested that the periphyton of macrophytes is a major path of gaseous N flux within the várzea (KERN & DARWICH 1997).

The objectives of this study are to identify the hydrochemical conditions under which N_2 fixation may occur and the extent to which periphytic N_2 fixation may yield benefits for the stands of macrophytes and possibly for the whole várzea.

Methods

Study area

Study sites were located on Marchantaria Island, 15 km upstream of the confluence of Negro and Solimões/Amazon Rivers near Manaus. This várzea island is inundated every year and has been the object of multidisciplinary studies since the early 1980s. The turnover of N in the várzea was studied with focus on the periphyton of macrophytes during rising water from April 3-12, 2001.

Sampling sites were along a transect from the Solimões River (station A), via the channel that links the river to the lake (station A-B), to the inner part of the island, to Lake Camaleão (station B, D, E, see Fig. 1). The stations used were those described by FURCH et al. (1983). Moreover, a newly formed lake in the young sedimentation area of Marchantaria Island, which is called Lake Novo by local people, was included in this study. The water level was related to the level of Negro River at Manaus and ranged between 26.22 m and 26.44 m a.s.l.

Water chemistry

Lake and river water were sampled at the surface and transported to the laboratory in polyethylene bottles in a cooler. The pH was measured with a glass electrode immediately after sampling in the field. Measurements of temperature and dissolved oxygen were conducted *in situ* with a polarographic electrode. Electrical conductivity was measured *in situ* using a platinum electrode. NO_3^- and NH_4^+ were determined from filtered samples (Sartorius SM 111, pore size 0.45 µm). NH_4^+ was measured by the indophenol blue method, and NO_3^- by the sulfanilamide method after reduction to NO_2^- with copperised Cd (GRASSHOFF et al. 1983). The sum of NH_4^+-N and NO_3^--N was defined as dissolved inorganic nitrogen (DIN) in this study.

N_2 fixation and CH_4 production

Three macrophyte species were selected for incubation of periphyton i.e. *Paspalum repens* BERG., *Echinochloa polystachya* (H.B.K.) HITCH. and *Eichhornia crassipes* (MART.) SOLMS. Each incubation assay of *Paspalum* and *Echinochloa* contained all roots, which were separated together with the periphyton from one node of the submerged stem. In the case of *Eichhornia* only one part of the root cluster was incubated. The dry weight (DW) of each root-periphyton complex, which was determined gravimetrically after drying at 105 °C ranged between 200 and 500 mg.

N_2 fixation was measured by the acetylene reduction method according to HARDY et al. (1968). 160 ml incubation vessels were filled to 130 ml with lake water. After injection of 5 ml C_2H_2 we obtained a 15 % vol acetylene atmosphere. Incubations were performed under light and dark conditions, each with 5 replicates, and were stopped after 3 hours by the addition of 1 ml formaldehyde. CH_4 production was measured in the same incubation vessels filled with water and periphyton. CH_4 production was closely related to the sample station, but not to macrophyte species and light conditions. Therefore, all CH_4 production data that were derived from the same station were pooled. At the end of incubation the headspace was sampled with 7 ml vacutainers. Analyses were carried out by a gas chromatograph equipped with a FID for detecting hydrocarbons (C_2H_4, CH_4).

For calculation of daily N_2 fixation rates, rates derived from light and dark incubations were assumed for 12 hours each. For *Echinochloa polystachya*, only 30 % of the light rate was considered because at a water level between 26 and 27 m a.s.l. approximately 70 % of the plant nodes with their root periphyton complexes were located below the euphotic zone, which comprises a mean depth of 1 m at Lake Camaleão (FURCH et al. 1985).

Biomass of the root-periphyton complex

Calculation of biomass was based on randomized sampling on April 11, 2001 at station A-B. Roots of *Paspalum* and *Eichhornia* with attached periphyton were sampled from 1 m^2. Sampling 1 m^2 of *Echinochloa* was more difficult because the long stems are branched and rooted in the sediment. Therefore, one whole plant of *Echinochloa* was taken and the number of nodes was related to plant densities obtained by KERN (1995). The dry weight of the total root-periphyton complex of each plant species was determined gravimetrically after drying at 105 °C.

In order to complete our own data for a final N budget of the three macrophytes, data concerning standing biomass, biomass production and plant N contents was taken from HOWARD-WILLIAMS & JUNK (1977), CARIGNAN & NEIFF (1992), PIEDADE et al. (1992), JUNK & PIEDADE (1993) and KERN (1995). All studies were derived from floodplains of Central Amazonia except data by CARIGNAN & NEIFF (1992). To obtain the N content in the stand of each species, our biomass data of the root-periphyton complex were multiplied with the N content of each plant compartment and upscaled to 1 hectare. If not available from literature, missing data concerning biomass and N contents of the stand were supplemented by difference calculations. To elucidate the method of calculating the N budget of the macrophyte stands, the shoot biomass of a *Paspalum repens* stand was derived from the difference between total biomass of 16.4 t ha^{-1} given by JUNK & PIEDADE (1993) and root-periphyton biomass of 4.4 t ha^{-1} from this study (see Table 2). If the shoot biomass of 12.0 t ha^{-1} is multiplied with its N content of 1.57 % (HOWARD-WILLIAMS & JUNK 1977) we receive 188.1 kg N ha^{-1} for the shoots of a *Paspalum repens* stand. Adding 74.3 kg N ha^{-1} in the root-periphyton complex finally results in the total N of the *Paspalum repens* stand of 262.4 kg ha^{-1}.

Results

Water quality

The study was undertaken in April 2001 when the water level was below 27 m a.s.l. and Lake Camaleão was filled by the rising water of the Solimões River entering through one channel at station A-B. Water chemistry was characterized by a high O_2 supply in the river water of station A and at the main channel of Marchantaria Island at station A-B (Fig. 2). O_2 concentrations decreased along the transect of Lake Camaleão in line with the distance from the Solimões River from 4 mg O_2 l^{-1} to less than 1 mg O_2 l^{-1}. An inverse pattern of CH_4 production with a maximum value at the deepest lake station D reflected intensive decay of organic material.

Despite the inflow of river water and its diluting effect on lake water chemistry, we could still find a gradient of electrical conductivity and pH along the lake stations at a river level between 26.22 m and 26.44 m a.s.l. (Fig. 2). In contrast to the increase of the electrical conductivity along the transect within Lake Camaleão, there was a decrease in DIN concentrations with an inverse pattern of NH_4^+ and NO_3^- concentrations. DIN concentrations ranged between 15 and 35 µg l^{-1}. Such low concentrations in April 2001 should have enabled N_2 fixation at all stations under study. The same is valid for Lake Novo where similar physico-chemical properties were found.

Periphytic N_2 fixation

Periphyton in Lake Camaleão and Lake Novo consists primarily of filamentous algae and aquatic invertebrates that are attached to floating and adventitious roots of aquatic and semi-aquatic macrophytes. During the short-term study with rising water in 2001, N_2 fixation within the root-periphyton complex of macrophytes was variable. Depending on locality, macrophyte species, and light conditions, the mean N_2 fixation ranged from 0 to 821.3 nmol N g DW^{-1} h^{-1} (Table 1). Near the Solimões River at station A-B we found lowest average rates between 0 and 9.1 nmol N g DW^{-1} h^{-1}. This station was characterized by O_2 concentrations of about 4 mg O_2 l^{-1} and relatively high concentrations of DIN (Fig. 2). If DIN concentrations of 35 μg N l^{-1} are low enough to allow N_2 fixation, then O_2 may play an important role for controlling N_2 fixation. At concentrations above 2.5 mg O_2 l^{-1} we measured low or zero nitrogenase activities, which is in accordance with earlier studies (KERN 1995).

Compared to the station A-B, significantly more N_2 was fixed at all sample stations of Lake Camaleão (B, D, E) and in particular at Lake Novo. The optimal conditions for N_2 fixation appear to be provided by the periphyton of the floating macrophyte *Paspalum repens*, followed by *Echinochloa polystachya* and *Eichhornia crassipes*. In all cases there was a sharp decline in the rate of N_2 fixation, if periphyton was incubated in the dark. Only in the stands of *Paspalum repens* at station E of Lake Camaleão and at Lake Novo, did N_2 fixation also play an important role under dark conditions. That means that at these sites, N_2 fixation was not restricted to photoautotrophic cyanobacteria and was enabled also by heterotrophic bacteria.

On the basis of root-periphyton biomass per m^2, the overall N_2 fixation rates in both lakes were 2.170 μmol N m^{-2} d^{-1}, 201 μmol N m^{-2} d^{-1} and 7 μmol N m^{-2} d^{-1} in the stands of *Paspalum repens*, *Echinochloa polystachya* and *Eichhornia crassipes*, respectively.

Biomass in stands of macrophytes

Highest biomass of the root-periphyton complex was found in *Paspalum repens* with 442 g DW m^{-2} followed by *Echinochloa polystachya* with 233 g DW m^{-2} and *Eichhornia crassipes* with 25 g DW m^{-2}. If these data are upscaled and related to data from the literature we receive approximate values for total N in macrophyte stands (Table 2).

Discussion

Water body

Lake and river water can be distinguished by different physico-chemical parameters, such as O_2, pH, electrical conductivity and NO_3 as long the Solimões River does not flood Marchantaria Island entirely at a water level below 27 m a.s.l. During our study in April 2001 a relatively high electrical conductivity with concentrations of above 100 μS cm^{-1} was most visible at station E of Lake Camaleão and reflected the nutrient pool with enhanced concentrations from the preceeding low water period. Closed parts of várzea lakes tend to anaerobiosis and methanogenesis as found in our incubated root-periphyton complexes. The higher the rate of CH_4 production, the better the anaerobic conditions for N_2 fixation because O_2 sensitive nitrogenases may be built up. Furthermore, the supply of organic carbon, as indicated by CH_4 production, can meet the high energy demand required by heterotrophic N_2 fixers, as shown by ENRICH-PRAST & ESTEVES (1998) in adventitious roots of *Oryza glumaepatula*.

The pH decreases slightly towards the inner part of Lake Camaleão, probably due to an accumulation of primarily dissolved inorganic carbon such as HCO_3^- and CO_2 during the decomposition of organic material (FURCH & JUNK 1985). The impact of pH on N_2 fixation is excluded since the range between 6.5 and 7.0 is not known to affect N_2 fixers.

A considerable influence on N_2 fixation is given by DIN concentrations because high NH_4^+ concentrations have an inhibitory effect on nitrogenase activity. Inorganic N concentrations of 50-100 μg N l^{-1} are usually considered inhibitory (HORNE & COMMINS 1987). A study from Spanish rice fields reports on N_2 fixation when DIN concentrations are below a threshold limit of 1,000 μg N l^{-1} (QUESADA et al. 1997). At Lake Camaleão NH_4^+ concentrations of the surface water have a broad range between 10 and 3,000 μg l^{-1} during the entire hydrological cycle due to the water level. Lowest NH_4^+ concentrations ranging between 10 and 30 μg l^{-1} are measured at all lake stations every year during rising and high water levels, and NO_3^- concentrations are even lower (FURCH 1999). This means that these concentrations did not exceed a level that represses N_2 fixation during the main growth period.

By contrast, we suggest that the presence of O_2 is the most limiting factor for N_2 fixation in the várzea. High oxygen concentrations in the channel station (A-B) did not allow N_2 fixation but nitrification which is indicated by high NO_3^- concentrations (KERN et al. 2002). At rising water when Lake Camaleão is filled by NO_3^- rich river water a constant decrease to nearly undetectable NO_3^- levels along the lake from station B to station E can be observed. This phenomenon is found every year (FURCH 1999) and can be explained by both plant uptake and denitrification. Denitrification has already been measured in the root-periphyton complex of *Echinochloa polystachya* (KERN et al. 1998). Whether NO_3^- is also subject to plant uptake in considerable amounts has to be questioned (KERN, unpubl.).

Periphyton

Periphytic communities of white water habitats are dominated by green algae and by diatoms (PUTZ & JUNK 1997). Although N_2 fixing cyanobacteria usually contribute less than 20 %, it was shown at Lake Camaleão that periphyton plays an important role in the exchange of gaseous N compounds, during both rising and receding water (KERN et al. 1998). It is obvious that the N enrichment in the root-periphyton complex will also be beneficial for the whole plant when dissolved N compounds are uptaken via the adventitious or floating roots.

If the potential of N_2 fixation is to be evaluated, the structure of macrophyte layers and the growth of periphyton also have to be taken into consideration. Algal biomass near the riverine water inflow contributing to N_2 fixation may be reduced by deposition of silty solids on the roots, low light, and physical disturbance (ENGLE & MELACK 1990). Nevertheless the floodplain near the river sustains large quantities of aquatic macrophytes and associated periphyton, as documented by JUNK (1970), DOYLE (1991) and ENGLE & MELACK (1993). It is probable that a high load of suspended solids transported with the inflowing river water is rich enough in total N and total P, allowing high growth rates without additional N inputs from atmosphere. The submerged parts of macrophytes may filter suspended solids highly efficiently. Particularly *Paspalum repens*, which develops the greatest root cluster, plays a key role in filtering suspended solids from the river as shown by studies from Lake Calado (ENGLE & MELACK 1990). Near the river, the deposition of inorganic epiphytic material was 15 times higher compared to stations within the lake. It may be suggested that these aquatic microhabitats with their filtered nutrients represent an important step for some following successional stages in the várzea.

An allogenic succession due to the deposition of suspended solids plays a key role in low elevational ranges, in contrast to high elevational ranges such as the floodplain forest where different stages of an autogenic succession can be observed (JUNK & PIEDADE 1997). Presumably the allogenic succession in the várzea is often accompanied by an autogenic succession due to biological N_2 fixation by which sediments in low elevational ranges are enriched with N.

N supply in stands of macrophytes

Paspalum repens

Depending on the water level *Paspalum repens* may occur in the rooted form or in the floating form. Being rooted mostly in the sediment means easy access to the plant's major N reservoir, as for example reported for *Paspalum repens* stands in the Paraná floodplain (MAINE et al. 1999). This is a case, invalid in the várzea, in which this C_4 grass is mostly aquatic. We identified *Paspalum repens* as the aquatic species with the highest N_2 fixating and thus fertilizing potential among the three abundant macrophytes under study. If plant N is released primarily during low water periods when *Paspalum* stands are partially decomposed on dry sediments, sediments will be enriched by N. *Echinochloa polystachya* and other rooted macrophytes may profit from more fertile conditions in the sediment during subsequent growth periods.

Echinochloa polystachya

The high biomass production of *Echinochloa polystachya* requires a high N supply. Adventitious roots of submerged stems that provide free access to N from the water (PIEDADE et al. 1994) may explain why it is that *Echinochloa polystachya* is by far the most important macrophyte of the várzea in terms of coverage, biomass and productivity. This path, however, should not be overestimated as the N pool of the water can be neglected with regard to the amount of N required in a stand of *Echinochloa polystachya* (KERN & DARWICH 1997). Moreover, our study shows that periphytic N_2 fixation of *Echinochloa polystachya* has only a minor nutritional potential for the growing stand. Depending on the site it can be estimated at between 1 % and 12 % of the whole N demand of one stand (Table 2, Fig. 3).

Much more important for the high growth rate of *Echinochloa polystachya* is the sedimentary N source as reported for other wetlands (ANDERSON et al. 1997; MAINE et al. 1999). Due to high amounts of fine-grained silt and clay, várzea sediments have a high cation exchange capacity (IRION et al. 1997). Primarily NH_4^+ undergoes adsorption and desorption and the interstitial water with concentrations of up to 5 mg l^{-1}, NH_4-N becomes easily available via the primary roots that maintain their contact with the sediment. Earlier results had shown that during rising water there was a decrease by 53.6 g N m^{-2} in littoral sediments of station D (0-5 cm) during a time period of 141 days. At the same time, when both the water level and the rooted macrophytes were rising by 5 m, a demand of 16.5 g N m^{-2} was calculated for the growing stand of *Echinochloa polystachya* (KERN 1995). Similar results were derived from *Spartina* salt marshes in Virginia where ANDERSON et al. (1997) calculated a macrophyte uptake of 33 g N m^{-2} yr^{-1}. This leads to the conclusion that the sedimentary N supply of station D can explain the whole biomass production of *Echinochloa* *polystachya* at Lake Camaleão. Periphytic N_2 fixation and thus N uptake via adventitious roots may become more important during pronounced high water, when some primary roots are dying or detach from the sediment. This however is the time when most biomass of the *Echinochloa* stand has been built up.

If the sedimentary N pool is essential for the vigorous growth of *Echinochloa polystachya*, the question arises what is the origin of this N pool. On the basis of present knowledge two explanations may be given. One source derives from high elevational boundaries where KREIBICH (2002) found 16.1 kg N ha^{-1} yr^{-1} fixed from the atmosphere in the rhizosphere of legume trees. If this N is released it may be partially leached to low elevational ranges. Another source is the lakes high internal production and decomposition of biomass during the aquatic phase. As mentioned above, the species *Paspalum repens* with its N_2 fixing root-periphyton complex, seems to be of major importance due to its abundance. Finally *Echinochloa polystachya* itself contributes to the high nutrient level in the várzea by sequestering and storing dissolved nutrients during high water (FURCH & JUNK 1997).

Eichhornia crassipes

Nutrient storage also applies to the C_3 plant *Eichhornia crassipes* with its short doubling time of about 15 days in Amazonia (JUNK & HOWARD-WILLIAMS 1984). Native in Amazonia, it is considered to be ecologically important due to its habitat function and its O_2 supply. JEDICKE et al. (1989) measured a relatively high input of 116 mg O_2 h^{-1} m^{-2} through the floating roots, which might affect N_2 fixation. Correspondingly periphytic N_2 fixation plays a minor role in the floating roots of *Eichhornia crassipes* during the study period. However, N_2 fixation need not be restricted to the root zone, as shown by CARIGNAN & NEIFF (1992) who found N_2 fixation primarily associated with decaying litter of *Eichhornia*. The authors found twice the fixation rate of root-periphytic N_2 fixation we measured at Lake Novo. They concluded that nutrient recycling from sediments and meadow litter together with heterotrophic N_2 fixation was sufficient to sustain high productivity of *Eichhornia crassipes* for long periods without external N input by the river. The discrepancy between biomass of the stand and the net primary production (NPP) of *Eichhornia crassipes* reflects the short life span of this plant accompanied by a high turnover of organic material throughout the year. Consequently, a closed lake internal N cycle is suggested for this species.

N budget of macrophytes

Data of biomass and productivity of the three aquatic macrophytes under study are listed in Table 2. In terms of NPP *Echinochloa polystachya* is most productive, with up to 100 t ha^{-1} yr^{-1}, the highest value among all plants of the várzea as documented by PIEDADE et al. (1992). The standing biomass of *Echinochloa polystachya* is also rather high and can reach 70 t ha^{-1}, which is much greater than that compared to *Paspalum repens* and *Eichhornia crassipes*.

Most N was stored in the root-periphyton complex of *Paspalum repens* related to the bulk N of 262.4 kg N ha^{-1}. From the total N content in the stands we can estimate the potential of periphytic N_2 fixation for the N budget of each macrophyte species. If we extrapolate the data, which derived from the period of rising water to an annual basis, then N_2 fixation revealed a high input of 207.8 N kg ha^{-1} yr^{-1} and 235.7 N kg ha^{-1} yr^{-1} within the *Paspalum* stands at Lake Camaleão and Lake Novo, respectively (Fig. 3).

The maximum N input via periphytic N_2 fixation in the stands of *Echinochloa polystachya* was found to be at least one order of magnitude lower. Relatively little atmospheric N_2 was gained in the stand of *Eichhornia crassipes* where the N input did not exceed 1 kg ha^{-1} yr^{-1}. These results derive from a small time scale and represent the period of rising water. Extrapolation to a year may be justified if the mean daily N_2 fixation rate of 201 µmol N m^{-2} d^{-1} in the stands of *Echinochloa polystachya* is compared with the mean N_2 fixation rate of 590 µmol N m^{-2} d^{-1} received in *Echinochloa* stands during the period of receding water (KERN 1995).

According to the estimated N input via periphytic N_2 fixation (Fig. 3), which are related to the total N in the stands (Table 2), we obtain a simplified picture of the percentage N of the biomass that potentially derived from N_2 fixation (Fig. 4). That means that the atmospheric N_2 source is most important for the stands of *Paspalum repens* with contributions to plant N of up to 90 %. In contrast, the maximum contribution of N_2 fixation in the stands of *Echinochloa polystachya* and *Eichhornia crassipes* was much lower with 15 % and 5 %, respectively. The contribution of N_2 fixation to the biomass of macrophytes of a reservoir in the state of São Paulo was in the same range. There, the root-periphyton complex of *Nymphoides indica* and *Pontederia cordata* provided 2-10 % and 1-3 % of the total plant N, respectively (SANTOS et al. 1986).

It may be concluded that the fixation of atmospheric N_2 is a successful adaptive strategy to avoid N limitation in the stands of macrophytes, which cover a very dynamic ecotone within the várzea. By means of a lake input-export budget for total N it could be shown that about 8 % and 17 % were derived from N_2 fixation at Lake Calado (DOYLE & FISHER 1994) and Lake Camaleão (KERN & DARWICH 1997), respectively. Considering the data of Lake Camaleão of this study, the significance of N_2 fixation for the N budget of certain macrophytes seems to be even higher than had been expected beforehand. Although periphytic N_2 fixation was restricted to the closed parts of Lake Camaleão and Lake Novo during the study period, it indicates a high fertilizing potential for the whole várzea. Particularly young sedimentation areas such as Lake Novo may be positively affected by fixation of atmospheric N_2 and accumulation of organic material.

Pioneer species such as *Paspalum repens* appear to contribute considerably to N accumulation. Although, stands of floating macrophytes are often lost in the várzea by heavy floods and the river current, a part of the organic material of *Paspalum* stands will be left on exposed sediments and increase their fertility. In this way, young successional stages may be transformed to higher productive stages, which provide better nutrient availability for future stands of herbaceous and woody plants.

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Table 1: N_2 fixation rates in the root-periphyton complex of macrophytes on Marchantaria Island during rising water in April 2001. All data are expressed as nmol N_2 g DW^{-1} h^{-1}.

			near Solimões	L. Camaleão			L. Novo
			A-B	B	D	E	
				entrance	center		center
Paspalum repens		min-max	0-39.0	591.3-1,014.5	70.8-720.9	35.0-576.0	69.2-555.0
	light	**mean**	**9.1**	**821.3**	**306.9**	**148.5**	**264.5**
		SD	13.5	143.5	235.9	149.4	173.3
		n	10	5	10	10	5
		min-max	0-1.6	14.7-41.6	5.1-27.3	7.1-206.2	13.0-482.8
	dark	**mean**	**1.0**	**25.1**	**14.6**	**65.5**	**170.3**
		SD	0.5	8.9	7.8	63.4	166.0
		n	10	5	10	10	5
Echinochloa		min-max	0-3.6		3.5-101.6	3.1-32.9	116.3-723.4
polystachya	light	**mean**	**0.6**		**38.2**	**19.2**	**318.2**
		SD	1.1		31.1	11.5	216.5
		n	10		8	4	5
		min-max	0-0.7		0.8-6.1	0.9-4.2	2.9-63.4
	dark	**mean**	**0.1**		**2.7**	**2.1**	**20.2**
		SD	0.2		1.6	1.2	22.3
		n	10		10	5	5
Eichhornia		min-max	0.1-4.3		0.8-33.5	1.7-51.8	10.4-64.7
crassipes	light	**mean**	**1.2**		**6.0**	**20.9**	**25.8**
		SD	1.5		9.3	18.7	19.9
		n	10		10	5	5
		min-max	0-0.1		0-8.2	0.8-2.9	0.7-13.1
	dark	**mean**	**0.0**		**3.3**	**2.1**	**7.3**
		SD	0.0		2.7	0.8	5.0
		n	10		10	5	5

Table 2: Net primary production (NPP), biomass and its nitrogen content in macrophyte stands of South American floodplains. Values are based on dry weight.

Species	NPP t ha^{-1} yr^{-1}	Biomass of the stand t ha^{-1}	N content of biomass %	Total N in the stand kg ha^{-1}
Paspalum repens				
shoots		12.0	1.57±0.30 [3]	188.1
root-periphyton complex		4.4 [1]	1.68±0.46 [2]	74.3
total	<50 [4]	16.4 [4]		262.4
Echinochloa polystachya				
shoots			1.47±0.20 [3]	248.4 [5]
root-periphyton complex		2.3 [1]	2.15±0.57 [2]	50.3 [5]
total	<100 [5]	<70.0 [5]		298.4 [5]
Eichhornia crassipes				
shoots		1.4	1.83±0.02 [3]	25.9
root-periphyton complex		0.3 [1]	1.62±0.08 [2]	4.1
total	10-15 [6]	1.7		30.0 [6]

[1] KERN & DARWICH, this study
[2] KERN, 1995
[3] HOWARD-WILLIAMS & JUNK, 1977
[4] JUNK & PIEDADE, 1993
[5] PIEDADE et al., 1992
[6] CARIGNAN & NEIFF, 1992

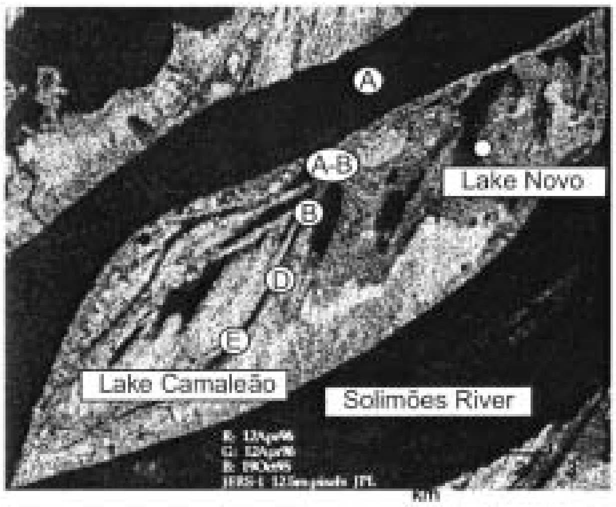

Fig. 1:
Study sites on Marchantaria Island. Young successional stages are found at the north-eastern part of the island in the surrounding of Lake Novo.

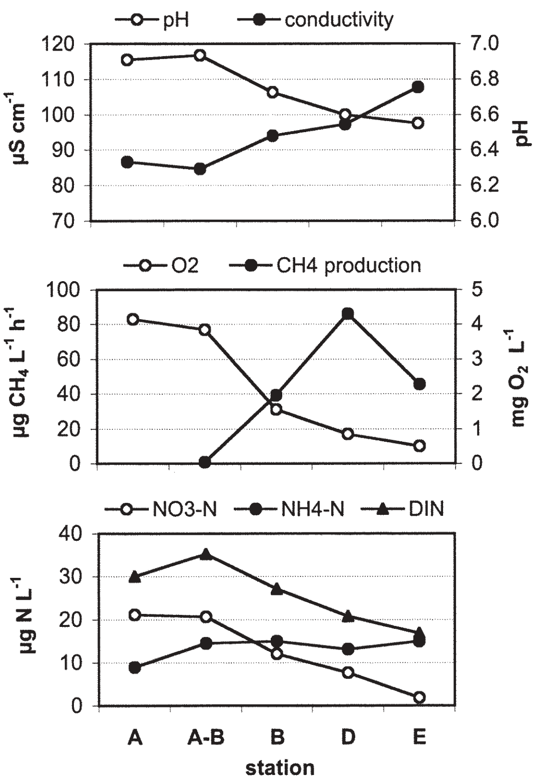

Fig. 2:
Physico-chemical properties along the transect from Solimões River (A) to Lake Camaleão (B, D, E) between April 3-12, 2001. Water level was 26.22-26.44 m a.s.l.

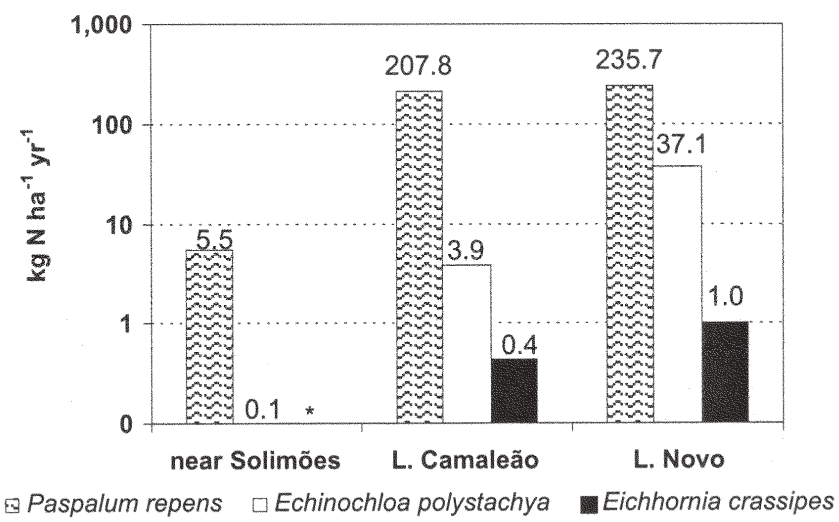

Fig. 3:
Estimated nitrogen input via periphytic N_2 fixation (* below detection limit).

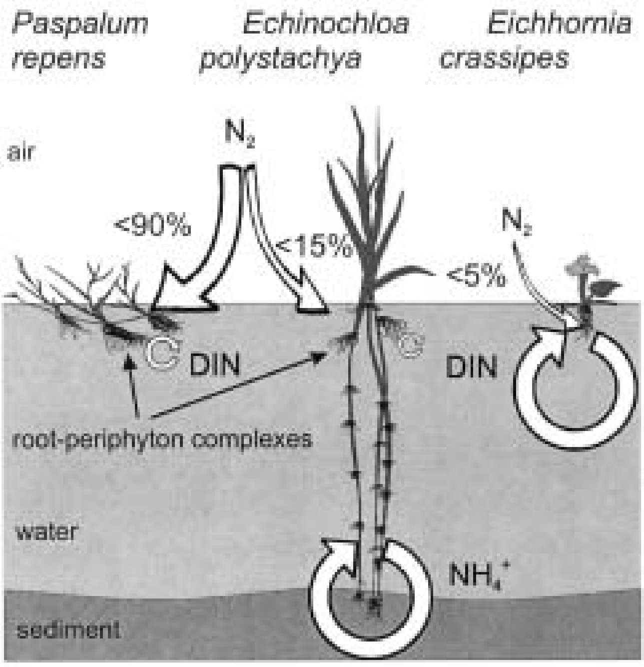

Fig. 4:
Nitrogen sources for the growth of macrophytes in the Amazon floodplain. Arrows indicate the estimated importance for the nitrogen budget of macrophyte stands.