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Nutrient dynamics in the floodplain ponds of the Paraná River (Argentina) dominated by the water hyacinth *Eichhornia crassipes.*

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Abstract. Some aspects of nutrient status and dynamics prevailing during low and high water conditions in the fringing floodplain ponds of the Paraná River dominated by the floating macrophyte *Eichhornia crassipes* are described. During summertime low water conditions, low DIN:DRP ratios (0.16—1.0) and low DIN (0.5—4.8 μmol.liter^{-1}) in the root-zone of the floating meadows suggest that macrophyte growth is limited by nitrogen. DRP concentrations appear to be controlled more by abiotic sorption-dissolution than by biological reactions. Preflood nutrient fluxes from the sediments, as estimated from pore-water profiles, show that a minimum of 1.19 and 0.38 mmol.m^{-2}.d^{-1} of DIN and DRP were regenerated from the sediments, respectively. Heterotrophic N_2 fixation is primarily associated with decaying litter (0.4 to 3.2 μmolN$_2$.g^{-1}.d^{-1}). Nutrient recycling from sediments and meadow-litter, and heterotrophic N_2 fixation (1.4 mmolN.m^{-2}.d^{-1}) appear sufficient to sustain high floating macrophyte productivity for long periods of time, without invoking large inputs from the river. The high water and early isolation periods are characterized by a very dynamic behavior of DIN, reflecting marked imbalances between N supply and demand by the biota. After hydrologic isolation of the ponds, DIN rapidly decreases to undetectable levels and stays low for the following 3 weeks, presumably as a result of high demand by phytoplankton and sediment bacteria. DIN increases again to high values 3—8 weeks after the flood, following the re-establishment of NH_4^+ fluxes from the sediments. Compared to DIN, DRP concentrations remain relatively high and change little during and after the flood. Because of their small amplitude and short duration, floods do not appear to stimulate floating macrophyte production in the Paraná.

Introduction

The Paraná River drains the second largest watershed in South America after that of the Amazon, covering an area of 3.1 × 10^6 km^2 shared by five countries: Brazil, Argentina, Paraguay, Bolivia and Uruguay. For a large part of its course, the Paraná is bordered by a ≈ 120,000 km^2

(Welcomme 1990), 10—50 km wide floodplain occupied by sub-tropical gallery forest, wetlands and numerous water bodies delimited by a complex network of alluvial levées. Dish lakes and oxbow lakes formed by meandering tributaries entering the floodplain are also common. At the latitude of Corrientes (Argentina), water bodies are typically linear to crescent-shaped (100 to 500 m wide, 500 to 3,000 m long), shallow (1 to 5 m), turbid (Secchi depths of 0.2 to 1 m), and rarely have direct hydrologic contact with the river. Compared to the Amazon and the Orinoco, the Paraná has an irregular hydrologic regime. Floods may occur 1—3 times per year for periods of 2 wk to 3 mo, and water level fluctuations are relatively small (2—6 m, Fig. 1). This behavior is apparently unrelated to the damming history of the Upper Paraná, which only began in the early 1960s.

Ponds smaller than about 20 ha normally sustain relatively high biomasses of the floating macrophytes *Eichhornia crassipes, Salvinia herzogii* and *Pistia stratiotes.* Rooted macrophytes (*Eichhornia azurea, Victoria cruziana, Ludwigia peploides, Paspalum repens* and *Panicum elephantipes*) are occasionally present (Neiff 1986). Of these species, *E. crassipes*, the water hyacinth, is by far the most important in terms of coverage, biomass and productivity. It normally forms cohesive floating meadows which may cover 20—100% of the available surface, with standing stocks (dry weight) ranging from 5 to 30 metric tons per hectare ($t.ha^{-1}$), (Perez del Viso et al. 1968, Neiff & Poi de Neiff 1984). The meadows are normally not anchored, and often accumulate on windward sides of the ponds. Production shows a pronounced seasonality. Biomass usually increases from October to March, and declines to about 50% of its annual maximum during the cool season (April to September). Net biomass increments of 10—15 $t.ha^{-1}$ are observed during the growth period (Lallana 1980; Neiff & Poi de Neiff 1984). Between exceptional floods (5—10 years), *Eichhornia* meadows may develop a floating organic soil and become colonized by other rooted hydrophytes.

Because of the absence of direct connections with the main channel, their low drainage ratio (drainage area:lake area of 0.5 to 1), and the importance of *E. crassipes* meadows, these water bodies differ markedly from previously described floodplain lakes in the Amazon and the Orinoco (Devol et al. 1984; Fisher & Parsley 1979; Fisher et al. 1988; Hamilton and Lewis 1987; Howard-Williams & Junk 1976; Lenz et al. 1986; Melack & Fisher 1990; Forsberg et al. 1988; Hamilton & Lewis 1990). Factors such as climate, flood regime and nutrient supply from the river, watershed and atmosphere may control the amplitude and periodicity of macrophyte production in floodplain lakes, but their relative

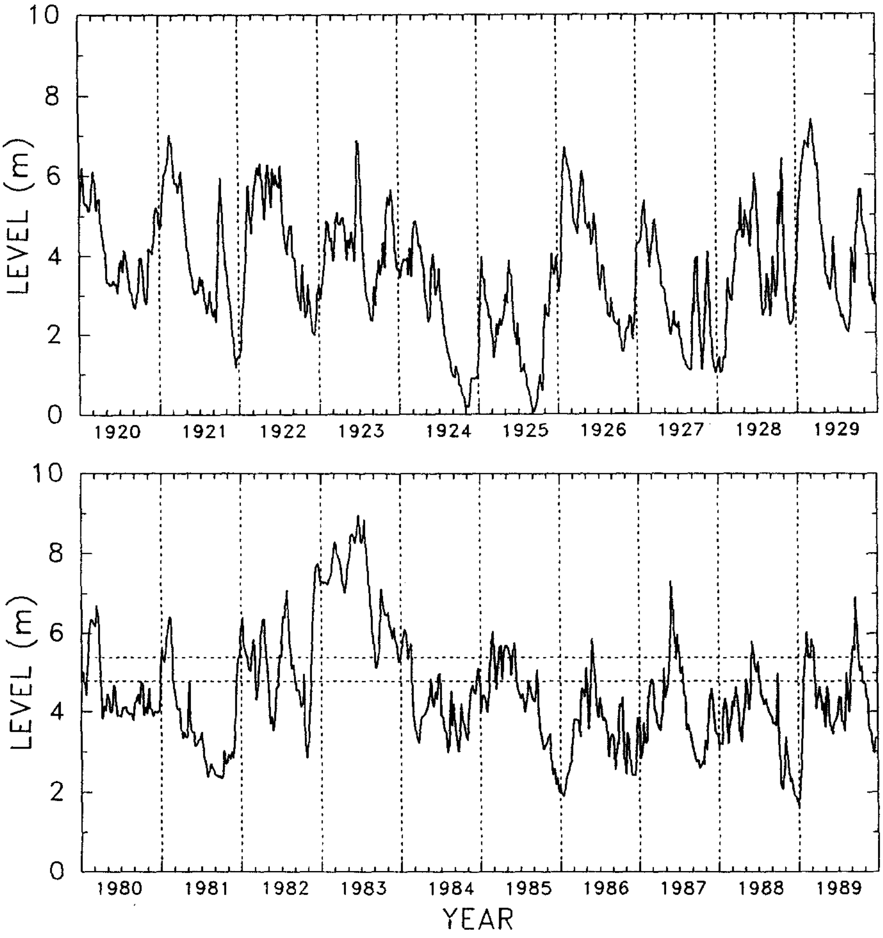

Fig. 1. Hydrometric level of the Paraná River at Corrientes during the 1920—1930 and 1980—1990 decades (source: unpublished data from the Argentina Direction of Navigation and Harbours). The horizontal lines show the approximate water ingression levels in Ponds San Nicolas South (4.8 m) and North (5.4 m).

importance in different floodplains is unclear. In the Paraná, the high seasonal growth rates observed in the ponds implies the existence of large nutrient sources. Nutrient supply from the river, during floods, has been invoked to explain the apparently high productivity of floodplain ponds and floodplains in general (e.g. Junk et al. 1989). The flood pulse hypothesis may, however, not apply to all floodplain systems, as internal and external sources may contribute substantially to support macrophyte production. The present report characterizes some of the major nutrient sources and pathways during low and high water conditions in the floodplain ponds of the Paraná and addresses the relative importance of river-derived nutrients *vs* other possible nutrient sources.

Study site

The study was conducted on the west bank of the Paraná River in Pond San Nicolas and four other nearby ponds on the fringing floodplain opposite the City of Corrientes (Argentina), 30 km downstream from the confluence of the Paraguay and Paraná Rivers (Fig. 2). Pond San Nicolas (27°27′S, 58°55′W; width ≈ 150 m, length ≈ 2 km) is located about 2 km from the river; it belongs to a complex of several similar ponds that are oriented parallel to the river. They are delimited by ≈ 50 m wide, 1—2 m high alluvial levées occupied by gallery forest. A road divides P. San Nicolas into two water bodies (San Nicolas North and San Nicolas South) which are chemically distinct at low water. Plant cover is usually more developed in the South (90—95% cover in 1984—1989) than in the North (50—80%). The depth of both segments is uniform, but varies with time from 1 to 5 m, depending on the river level. The ponds are indirectly connected to the river 1—3 times per year, when the water level of the Paraná reaches or exceeds the 4.8 m datum at Corrientes (Fig. 1). Water and fine particulate matter are exchanged with the outside during floods, but *E. crassipes* normally remains trapped by trees and shrubs growing on the levées. Significant macrophyte flushing to the river, as described by Bonetto (1986), appears to occur only during exceptional floods such as that of 1983.

The open water sections of the ponds are characterized by low Secchi depths (25—100 cm), a pH of 6.0 to 6.7, and low oxygen levels (0—50% of saturation). Mean monthy air temperatures vary seasonally between 16 °C in July and 27 °C in January. The phytoplankton of the open water is dominated by small green, cryptophycean and dinoflagellate algae and cyanobacteria (e.g. *Sphaerocystis, Microactinium, Rhodomonas, Peridinium, Merismopedia, Anabaenopsis*). Planktonic heterocyst-bearing cyanobacteria are notably rare. Planktonic primary production rarely exceeds 1 $gC.m^{-2}.d^{-1}$ (Zalocar et al. 1982), due to alternating light and nitrogen limitation (Carignan & Planas, unpubl.). The surrounding soil is composed of a superficial (0—50 cm) permeable layer of sandy silt underlain by ca. 2 m of compact reddish to grayish loam which is nearly dry to the touch. In the ponds, the loam is covered by 20—35 cm of dark, organic (5—10% C) and porous (ϕ = 0.8—0.95) sediments. The limited thickness of organic

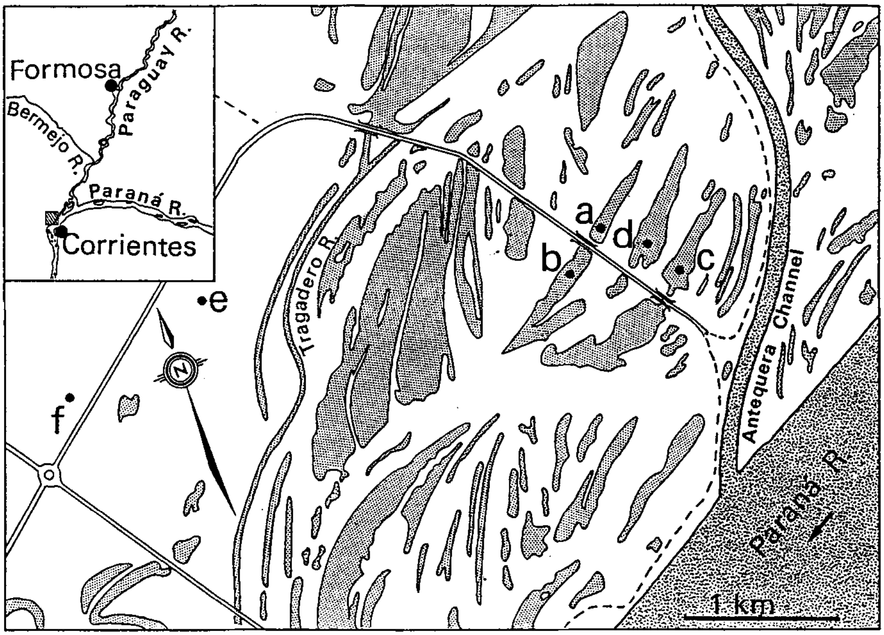

Fig. 2. Location of the study site, on the West bank of the Paraná River, Argentina; "a": Pond San Nicolas North; "b": Pond San Nicolas South; "c": Pond Puente North; "d": Pond Baltazar North; "e" and "f" are high water sampling stations.

sediments indicates that long term accumulation of organic matter does not presently occur in the ponds.

Methods

Water column, pore water and sediments

The site was visited during the warm season, between December and February 1988—1990, when macrophyte growth and nutrient demand are at maximum, and in April 1989 and 1990, when *E. crassipes* meadows are declining. The water column in floating meadows was sampled in December 1988 and April 1989 at four stations in Pond San Nicolas using passive equilibration devices ("peepers", Hesslein 1976; Carignan 1984) with a vertical resolution of 2 cm. Biologically inert polysulfone membranes (Gelman DM-200, 0.2 μm pore size) were used. The samplers were initially de-aerated by keeping them for at least 12 h in polyethylene bags inflated with 20 liters of nitrogen. They were positioned at least 50 m inside the meadows, and were left in place for one week in order to minimize disturbances resulting from their installation. Because this type of sampler requires about 24 h to reach equilibrium with the outside turbulent water, the chemical profiles thus obtained represent average conditions over 1—2 days. Horizontal profiles were taken at meadow edges to verify the existence of possible nutrient gradients between the open water and root environments. These profiles were taken at a depth of about 10 cm with 3 cm-wide diffusion samplers designed to penetrate the root mat without damaging the roots. Sediment porewater samples were obtained with a 1 cm vertical resolution by leaving diffusion samplers for 12—15 d in sediments; these samplers were carefully positioned by divers.

Dissolved inorganic carbon (ΣCO_2) and pH were measured following Carignan (1984). Samples for dissolved organic carbon (DOC), nutrients and major ions were collected in pre-acidified polystyrene tubes (1N Ultrex HCl, final pH $\approx$ 3, stored at 4 °C) and analyzed within 2 weeks. DOC was measured by conductimetry after UV-persulfate oxidation. Sulfate was measured by ion chromatography; NH_4^+, NO_3^- + NO_2^- (henceforth called NO_3^-) and dissolved reactive phosphorus (DRP) were measured by automated methods (Stainton et al. 1977); total dissolved Fe, Mn, Na, K, Ca and Mg were measured with a Jarrell AtomScan 25 plasma emission spectrometer. Dissolved oxygen was measured with a YSI polarographic probe.

In January—April 1990, nutrients and major ions (unacidified samples) in surface waters were followed during and after an exceptional flood event during which the water-level reached the 8 m datum at Corrientes. On average, such floods occur only every 5—10 yr. Duplicate water samples were collected between 10:00 and 12:00 every second day in the floodplain and the river, and kept for 2—3 h on ice in polyethylene bottles. Samples were filtered through pre-washed Gelman HT-450 (0.45 μm) membranes for DRP, and Gelman AE glass fiber filters for NH_4^+ and NO_3^- manual determinations (Stainton et al. 1977) with five or ten cm cuvettes. Total P was measured after autoclaving (45 min at 120 °C) 50 ml samples with 0.5 g of potassium persulfate. We have not determined the efficiency of this procedure, but Engle and Sarnelle (1990) have reported that a 30 min digestion time with a smaller quantity (0.3 g) of alkaline persulfate (Valderrama 1981) underestimated TP in turbid waters of the Amazon.

Vertical temperature profiles were recorded every 15 min at 10—20 cm intervals during low-water between November 1989 and January 1990, and between December 1990 and January 1991 using thermistor chains assembled with YSI 46032 glass-encapsulated thermistors set with epoxy in 25 × 4 mm steel shells. YSI cable and Electro Oceanics connectors were used to connect the cables to Licor LI-1000 data loggers enclosed in submersible aluminium cases. Precision and absolute accuracies were 0.02 °C and 0.05 °C, respectively. Sediment cores were collected by divers at the same site in Pond San Nicolas N before (January 1989) and after (April 1990) the flood using 10 cm diameter tubes. The cores were sectioned at 2 cm intervals and freeze-dried. Total C and Total N were measured with a Carlo Erba CNS analyzer.

Heterotrophic N_2 fixation

Heterotrophic N_2 fixation was measured in April 1990 (acetylene reduction), and in January 1991 (acetylene and $^{15}N_2$; Knowles 1980, 1982). In April, samples were collected in the field (San Nicolas N, high DIN concentration), and from an established (6 mo.) *E. crassipes* colony kept in a 8 × 2 × 1 m outside concrete tank (low DIN) located in Corrientes. Because Pond San Nicolas had been experimentally fertilized with DIN in January 1991 (Carignan and Planas, unpubl.), samples were collected in adjacent Pond Baltazar (Fig. 2), where DIN was undetectable (<0.05 μmol.liter^{-1}). Water, live roots and submersed decaying leaves and petioles of *E. crassipes* (0.5—1 g DW) were sampled underwater with clean 500 ml Mason jars, well inside the meadows. The type of litter assayed varied from cohesive to highly decomposed leaves and petioles. One hundred ml of C_2H_2-saturated pondwater was slowly injected at the bottom of the jars with a long needle; displaced water was evacuated through a second shorter needle, and the jar was gently mixed. This procedure allowed C_2H_2 introduction with no visible disturbance of the microbial assemblage attached to the decaying vegetation. Alternatively, we found that 50 ml of C_2H_2-gas could be slowly injected with a fine hypodermic needle through the septum and completely dissolved by gentle agitation, with little disturbance of the attached microbial assemblage.

Incubations were carried out in the dark, at 21—32 °C, within 1 °C of ambient temperatures, for periods of 1.5—4 h. Subsamples (25 ml) were taken from the jars with a 50 ml glass syringe and dissolved C_2H_4 was stripped by vigorous agitation for 90 s using a 1:1 sample:air ratio. Five ml of the gas phase were then injected into vacutainers, and C_2H_4 measured with 10 d with a gas chromatograph equipped with a Porapak N column and a flame ionization detector. Proper temperature corrections and gas partition coefficients (Flett et al. 1976) were used to calculate C_2H_4 reduction rates. In all experiments, control jars containing litter and pondwater were run to measure natural C_2H_4 levels. Care was taken to avoid accidental contamination of samples with NH_4^+ and NO_3^- which inhibit N_2 fixation. The absence of detectable contamination was systematically verified by measuring initial and final NH_4^+ and NO_3^- concentrations in the jars.

Calibration of the C_2H_2 reduction technique was performed by injecting 5.00 ml of 99% $^{15}N_2$ in water-filled jars, incubating ≈ 2 h, after which time C_2H_2 was added, thereby inhibiting further uptake of $^{15}N_2$, and the jars incubated for another 2 h. Vigorous sample agitation for ≈ 60 s after injection of the $^{15}N_2$ was unavoidable here since immediate isotopic exchange with dissolved $^{14}N_2$ had to be insured. At the end of the C_2H_2 incubation, C_2H_4 was sampled as above, and the loose particulate matter was resuspended and subsampled for filtration through Gelman AE glass fiber filters. Litter material was dried at 65 °C, weighed, finely ground and analyzed for total N (Carlo Erba). ^{15}N in filters and plants was measured by mass spectrometry (VG SIRA-12) after combustion at 900 °C with Cu-CuO. The isotopic ratio of N_2 in the experimental vessels was calculated assuming that they were initially saturated (Weiss 1970) with atmospheric N_2 having a 0.3663% ^{15}N content. Total N (TN) and total dissolved N (TDN) were measured by persulfate oxidation (D'Elia et al. 1977) followed by direct reading of the ultra-violet absorbance of NO_3^- at 220 and 275 nm (Smith et al. submitted).

Denitrification

Denitrification within the *E. crassipes* meadow was assayed only once in the field in April 1989, at a water temperature of 22 °C, using acetylene to inhibit the final $N_2O \rightarrow N_2$ reaction (Chan and Knowles 1979). Ten to twelve plants were gently lifted from the water and placed in duplicate 100-liter, 0.22 m^2, plastic containers to which 80 liters of surface pondwater had been added. Plant density in the containers was similar to natural surrounding values. Ten liters of C_2H_2-saturated pondwater were then distributed within the root zone using plastic tubing. The containers were immediately covered with 1.5 m high, airtight tents made of two layers of 5 mil translucent polyethylene. The tents were tightly secured around the containers below the water-level; they enclosed 200—220 liters of air, to which 20 liters of C_2H_2 were added. The enclosed atmosphere and water column were then periodically sampled at three levels through lateral ports for the next 46 h. After 30 h, KNO_3 solutions were added through the lateral ports to raise NO_3^- concentrations to 9.8 in one container, and 98 μmol.liter^{-1} in the other. The low NO_3^- vessel was, however, damaged during a storm. Dissolved nitrous oxide was extracted by vigorous agitation (90 s) of equal volumes of air and water in 50 ml syringes. Gas samples were collected in vacutainers and analyzed within one week by chromatography using a Porapak Q column and an electron capture detector. Water samples for NO_3^- analysis were taken before and after the experiment, and measured within 2 h of collection.

Results and discussion

Major ions, nutrients and vertical mixing within floating meadows during the isolation phase

Vertical profiles of major ions, taken in December 1988 through the ≈ 50 cm thick floating *E. crassipes* root-mat, show that the ionic composition of San Nicolas N and S ponds is dominated by sodium and bicarbonate (e.g. San Nicolas S, Table 1). Major ions in both ponds bear the signature of the Paraguay River where Na > Ca > Mg > K compared to that of the Upper Paraná where Na ≈ Ca ≈ Mg > K (Bonetto & Lancelle 1981). This is to be expected since the waters of both rivers usually remain well separated at the level of Corrientes, 30 km below their confluence. The vertical distribution of several constituents (ΣCO_2, Ca, Mg, Na, Fe, Mn) is constant with depth which implies frequent mixing of the water column, at least over the upper 70 cm. Temperature profiles obtained during 94 days of the warm season (e.g. Fig. 3) show a complex mixing pattern dependent on daily wind and insolation. In open waters during sunny days, stratification typically begins around 10:00 AM and persists until 4:00 AM the following day. Complete mixing persists during cloudy and windy days. In the meadows, stratification tends to occur earlier and persists longer; complete mixing and upward dispersion of sediment-derived nutrients may occur only once every 1—2 weeks, during strong storms.

Although Ca, Mg and Na have orthograde profiles, NH_4^+, DRP, K and SO_4^{2-} maintain pronounced vertical gradients in meadows (Table 1 and Fig. 4) attributable to an intense biological activity taking place within the root-zone. The persistence of higher K concentrations within the root-mat may be due an exchange for NH_4^+ by the root system, as we have observed equivalent release of K during NH_4^+ uptake experiments with *Eichhornia* (Carignan et al. unpubl.). Nitrate was normally not detectable (at the 0.05 μmol.liter^{-1} level) at any time or depth in the floating meadows. The disappearance of SO_4^{2-} around 15 cm, and the presence of high dissolved Fe concentrations, defines an anoxic and reducing environment confirmed by the absence of detectable dissolved oxygen below 5—10 cm. Compared to plant-covered areas, open waters are characterized by the presence of

Table 1. Vertical profiles of ΣCO_2, DOC and major ions through the floating meadow in Pond San Nicolas South in December 1988. Data for the Upper Paraná and Paraguay Rivers are from Bonetto and Lancelle (1981)

Depth	ΣCO_2	DOC	Ca	Mg	Na	K	Fe	Mn	SO_4^{2-}
(cm)					(mmol.liter^{-1})				
0	1.32	2.74	0.29	0.22	1.03	0.14	0.005	0.001	0.0278
2	3.50	1.77	0.33	0.24	1.03	0.08	0.053	0.009	
4	3.63	1.74	0.34	0.25	1.03	0.10	0.070	0.010	0.0195
6	3.58	1.82	0.35	0.25	1.01	0.11	0.058	0.011	
8	3.58	1.74	0.35	0.25	0.98	0.11	0.056	0.011	
10	3.61	1.80	0.35	0.25	1.03	0.11	0.053	0.011	0.0140
14	3.57	1.87	0.35	0.25	1.05	0.11	0.056	0.011	
18		1.72	0.36	0.25	1.05	0.10	0.057	0.010	0.0003
20	3.64	1.73	0.35	0.25	1.05	0.10	0.054	0.009	
24		1.70	0.35	0.25	1.03	0.08	0.054	0.009	0.0000
26	3.72	1.70	0.35	0.25	1.01	0.07	0.057	0.009	
30		1.25	0.34	0.25	1.07	0.07	0.058	0.009	0.0000
34	3.83	1.57	0.35	0.25	1.01	0.05	0.063	0.009	
43		1.46	0.34	0.24	1.05	0.04	0.056	0.008	0.0000
49	3.64	1.44	0.33	0.24	1.01	0.03	0.054	0.007	
52		1.47	0.33	0.24	1.01	0.03	0.054	0.007	0.0000
58	3.40	1.44	0.33	0.24	1.01	0.03	0.054	0.007	
64		1.52	0.33	0.24	1.01	0.03	0.053	0.007	
Paraguay			0.32	0.20	0.84	0.08			
Upper Paraná			0.11	0.11	0.11	0.03			

3—6 ppm of dissolved oxygen at the surface, higher turbidity, and generally undetectable DIN concentrations (Carignan et al. 1992).

Vertical nutrient profiles taken through and below the root zone in summer (Fig. 4) suggest that DIN concentrations may limit the growth of *E. crassipes*. No comparable profiles for the floating meadows of the Amazon or Orinoco could be found in the literature. Ammonium levels (0.5—4.8 μmol.liter^{-1}) within the ≈ 50 cm-thick root zone in both ponds are much lower than those generally reported for environments where this plant is abundant, and orders of magnitude lower than concentrations previously used to establish relationships between growth and nutrient concentrations for tropical floating macrophytes (Gopal 1987). Low (0.1—0.6 μmol.liter^{-1}) DIN concentrations were also observed within the root-zone of floating meadows in two other ponds (Carignan et al. 1992). The success of *E. crassipes* in the Paraná shows that it can adapt to low nutrient concentrations and that supply is more important than concentra-

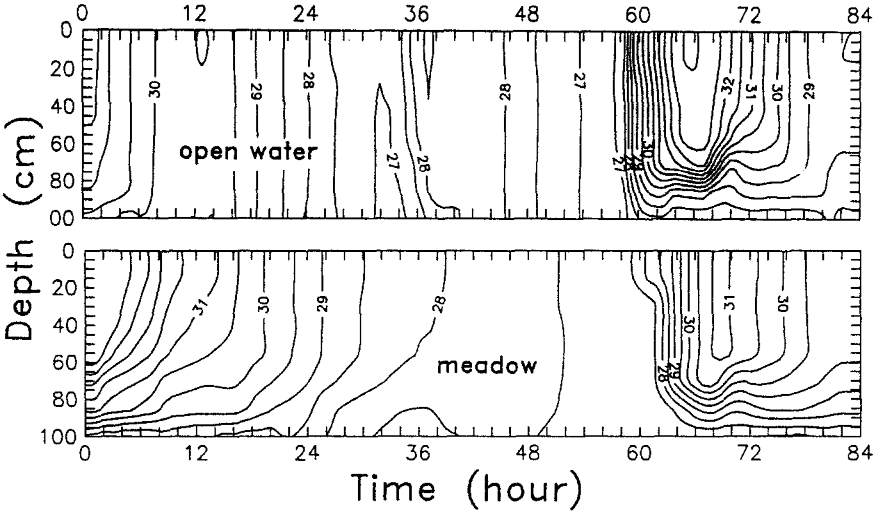

Fig. 3. Temperature isopleths in open waters and under an *E. crassipes* meadow from January 9 to 12, 1990; t_0 is midnight, January 9. January 8 was calm and sunny, and was followed by two cloudy and windy days; sunny and calm conditions returned on January 11. The vertical thermistor chains were placed about 100 m apart, on each side of the open water/meadow boundary.

tion in determining its growth in natural systems. The low DIN:DRP ratios (0.16—1.0) observed within the root zone are far from the ≈ 16:1 proportion required by plants, and rule out P as a potential limiting nutrient in these ponds. We have experimentally verified (Carignan et al. 1992), using 20 m^2 limnocorrals, that production by *E. crassipes* is in fact N-limited during the warm season. Dissolved organic nitrogen concentrations in open- and meadow-water range between 50 and 70 μmol.liter^{-1}. The origin, lability and fate of this pool are presently unknown.

Even if temperature and major ion data indicate that the upper 40 cm of water column is well mixed (Fig. 3), closely spaced NH_4^+ maxima and minima are present in the upper 10 cm (Fig. 4). The presence of steep NH_4^+ gradients strongly suggest that organic-N mineralization occurs concurrently with reassimilation within this zone. Established meadows thus appear to recycle NH_4^+ rapidly within the upper root mat, where decaying litter (leaves and stems) is abundant (Neiff & Poi de Neiff 1984).

During the cool season, nutrient concentrations under the plants increase by a factor of 10 (Fig. 4). This increase is likely attributable to the coincident decline in plant biomass which normally begins in April. The reasons behind the timing of the plant decline are unclear, but probably involve increasing grazing by insects, decreasing insolation, and lower temperatures, which decrease below the optimal 20—30 °C range reported

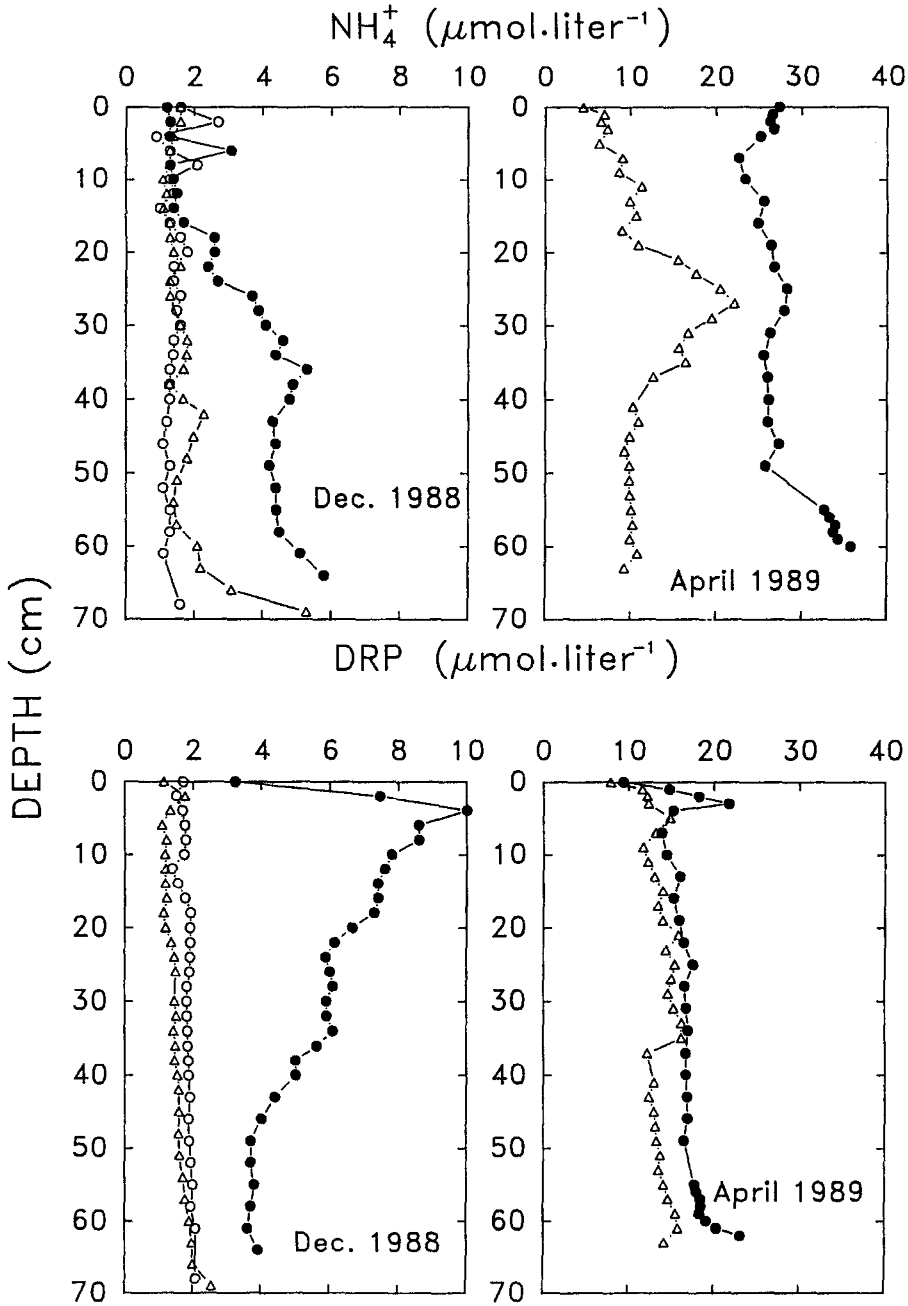

Fig. 4. Vertical profiles of NH$_4^+$ and DRP through the ≈ 50 cm thick root-zone of *E. crassipes* meadows in ponds San Nicolas North (open symbols) and San Nicolas South (filled symbols) in summer (December 1988) and winter (April 1989).

for *E. crassipes* by Sato (1988). Although no data are available, nutrient concentrations are expected to reach even higher values in July—August, when biomass reaches its annual minimum.

Horizontal NH_4^+ and DRP profiles taken at a depth of 10 cm across the open water/root zone interface during the growing season show further evidence of spatial heterogeneity in nutrient production and uptake within the litter and upper root zone (Fig. 5). DRP and NH_4^+ tend to be present in higher concentrations inside the root zone than in open water. Although actual nutrient fluxes across this interface cannot be evaluated, the profiles suggest that dissolved nutrients are lost from the upper root zone to the open water, even during periods when macrophyte growth and nutrient

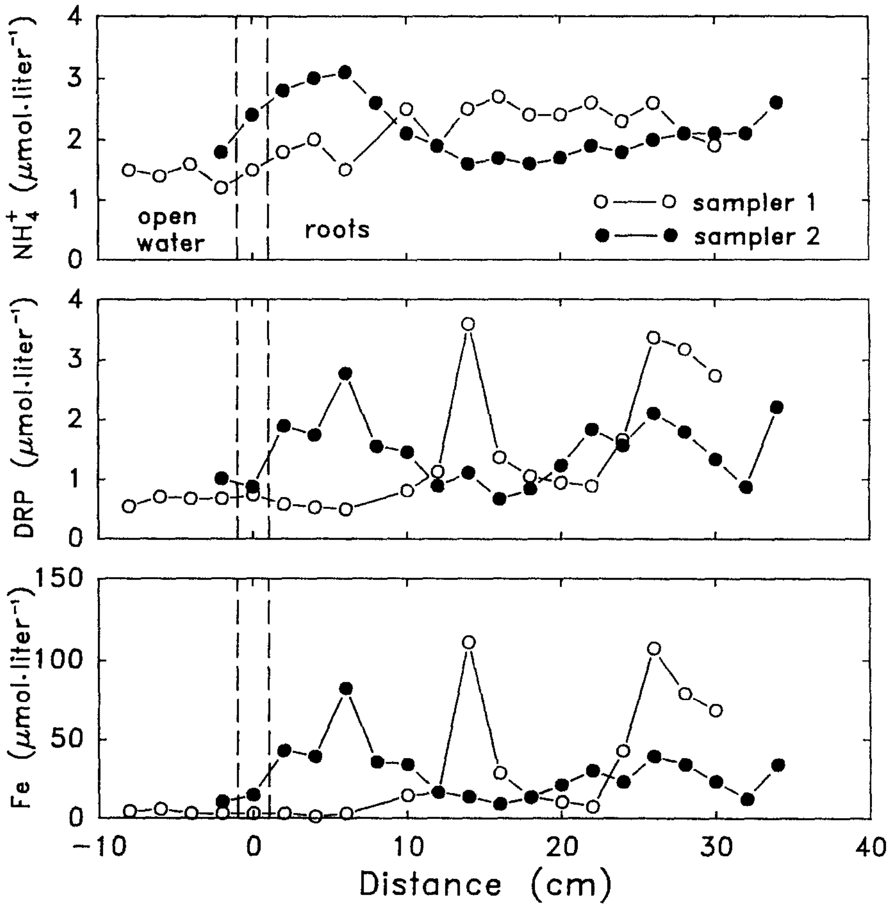

Fig. 5. Horizontal profiles of NH_4^+, DRP and total dissolved Fe across the open-water/root zone boundary of the floating meadow in Pond San Nicolas North in December 1988.

demand are high. A strong linear relationship is observed between DRP and dissolved Fe for the horizontal profiles (DRP = 0.029 Fe + 0.61, $r^2 = 0.94$, $n = 38$). The high Fe concentrations most probably arise from the reduction of Fe-oxyhydroxides which are frequently visible on root hairs and plant debris near the water surface. The DRP-Fe regression suggests that 0.029 moles of P is liberated for each mole of Fe reduced. This ratio (1.7% by weight) is well within the range of reported values for phosphate adsorption onto iron oxyhydroxides (Sholkovitz & Copeland 1982). A similar relationship (DRP = 0.029 Fe + 0.073, $r^2 = 0.86$, $n = 97$) is maintained when the summertime vertical profiles through the root zone in San Nicolas N are added to the analysis. Thus, DRP concentrations in the root zone appear to be strongly influenced by phosphate adsorption onto Fe oxyhydroxides. Such a behavior is expected in systems where P is supplied in large excess of biological demand.

Pore water chemistry and internal nutrient fluxes

We used the chemical gradient approach to estimate nutrient fluxes at the sediment-water interface, and summed that transport was due to molecular diffusion only. Fluxes were calculated as:

$$J|_0 = -\phi D_s \frac{\mathrm{d}C}{\mathrm{d}x} \qquad (1)$$

where $J|_0$, is the flux at the interface ($\mathrm{mol.cm^{-2}.s^{-1}}$), $\mathrm{d}C/\mathrm{d}x$ is the concentration gradient ($\mathrm{mol.cm^{-4}}$), ϕ is the sediment porosity, and D_s is the coefficient of molecular diffusion ($\mathrm{cm^2.s^{-1}}$) corrected for tortuosity using $D_s = D_m/\phi F$ (Berner 1980) with $F = \phi^{-3}$ for fine-grained sediment (Andrews & Bennett 1981; Ullman and Aller 1982), where D_m is the temperature-corrected self-diffusion coefficient (Li & Gregory 1974). It should be stressed that fluxes calculated in this manner probably underestimated true fluxes since bioturbation, bioirrigation and methane ebullition may have contributed to solute transport. Nevertheless, the exercise provides a first estimate of the importance of nutrient recycling from the sediments in such systems.

The results (Fig. 6, Table 2) suggest that on average, at least 1.10 $\mathrm{mmol.m^{-2}.d^{-1}}$ of NH_4^+ and 0.27 $\mathrm{mmol.m^{-2}.d^{-1}}$ of DRP were released from the sediments before the exceptional flood of January-February 1990. The low N:P flux ratio of 4.1 shows that, relative to biological demand, P is internally supplied in large excess to N in the ponds. Release is more variable for DRP than for NH_4^+, but no clear seasonal differences are observed.

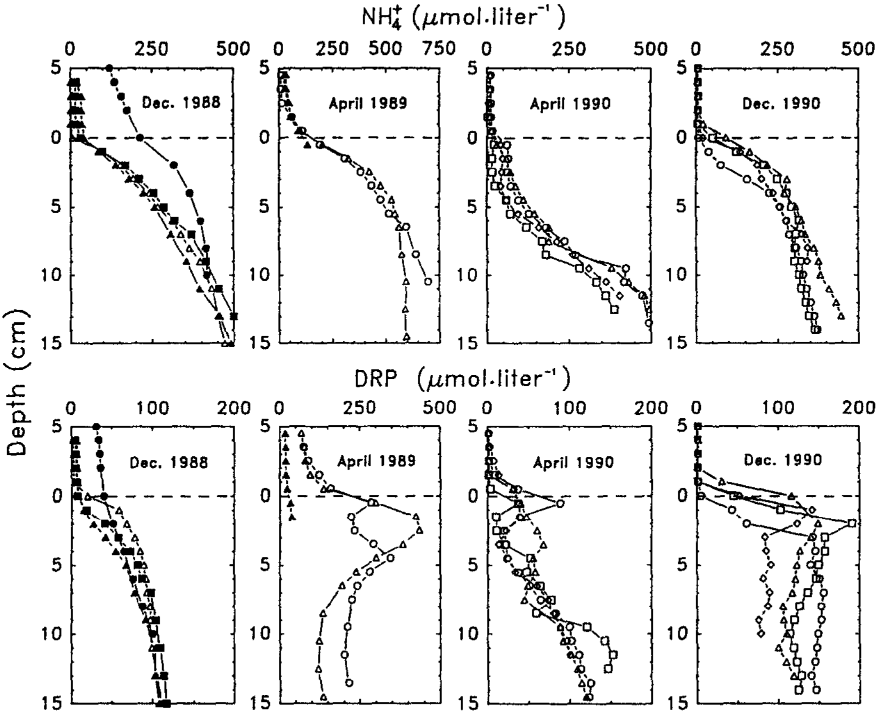

Fig. 6. Concentrations of NH$_4^+$ and DRP in the sediment pore-waters of ponds San Nicolas North and South under floating meadows (filled symbols) and in open water (open symbols).

The April 1990 profiles, taken 60 d after the flood differ markedly from those observed on other dates, and suggest a decrease in NH$_4^+$ flux at the interface compared to earlier dates. Two possible causes may explain the peculiar concave-upward shape of the NH$_4^+$ profiles (Fig. 6): biological disturbance or irrigation of the upper ≈ 8 cm, or the recent deposition of about 5—10 cm of NH$_4^+$-absorbing material. There is no reason to believe that invertebrate activity should have been particularly high at that time, compared to December 1990, when the ponds still had a very reduced macrophyte cover and oxygen was present in the water column. The transient relaxation of pore-water NH$_4^+$ following a major, flood-induced disturbance of the upper 10 cm appears more plausible. Two different mechanisms may be invoked here. First, because NH$_4^+$ is subject to reversible adsorption in soils and sediments, the possible rapid deposition of 5—10 cm of new sediments during the flood may have left a NH$_4^+$-depleted surficial layer; pore-water NH$_4^+$ originating from decomposition would then tend to increase with time, but adsorption onto the NH$_4^+$-depleted solid phase would slow the process. Secondly, it is also possible

Table 2. Concentration gradients and NH_4^+ and DRP fluxes and ratios across the sediment-water interface in ponds San Nicolas North and South. The fluxes are based on bottom temperatures of 20 °C and 26 °C in April and December, respectively. A sediment porosity of 0.95, calculated assuming a density of 2.6 for the sediment solids, was used. Diffusion coefficients used in DRP flux calculations assume that DRP is equivalent to orthophosphate, and are composite coefficients taking into account the relative proportions and specific diffusion coefficients (Li & Gregory 1974) of $H_2PO_4^-$ and HPO_4^{2-} at *in situ* pH

Station	Date	Plants	Gradient (μmol.cm^{-4})		D_s (cm^2.s^{-1})		Flux (mmol.m^{-2}.d^{-1})		DIN:DRP
			NH_4^+	DRP	NH_4^+	DRP	NH_4^+	DRP	
South-1	15 Dec 1988	yes	0.053	0.0054	1.83E-5	7.77E-6	0.80	0.03	23.1
North-1	15 Dec 1988	no	0.096	0.0391	1.83E-5	7.69E-6	1.44	0.25	5.8
North-2	15 Dec 1988	yes	0.070	0.0208	1.83E-5	7.69E-6	1.05	0.13	8.0
North-3	15 Dec 1988	yes	0.053	0.0113	1.83E-5	7.69E-6	0.80	0.07	11.2
North-8	20 Apr 1989	no	0.117	0.1280	1.56E-5	6.55E-6	1.50	0.69	2.2
North-9	20 Apr 1989	no	0.123	0.1250	1.56E-5	6.55E-6	1.58	0.67	2.3
South-2	20 Apr 1989	yes	0.044	0.0102	1.56E-5	6.61E-6	0.56	0.06	10.2
North-1	30 Apr 1990	no	0.044	0.0517	1.56E-5	6.55E-6	0.56	0.28	2.0
North-2	30 Apr 1990	no	0.008	0.0290	1.56E-5	6.55E-6	0.10	0.16	0.7
North-3	30 Apr 1990	no	0.023	0.0179	1.56E-5	6.55E-6	0.29	0.10	3.0
North-4	30 Apr 1990	no	0.009	0.0352	1.56E-5	6.55E-6	0.12	0.19	0.6
North-1	16 Dec 1990	no	0.080	0.0813	1.83E-5	7.69E-6	1.20	0.51	2.3
North-2	16 Dec 1990	no	0.073	0.0984	1.83E-5	7.69E-6	1.10	0.62	1.8
North-3	16 Dec 1990	no	0.115	0.0892	1.83E-5	7.69E-6	1.73	0.56	3.1
North-4	16 Dec 1990	no	0.085	0.0874	1.83E-5	7.69E-6	1.28	0.55	2.3
Mean flux (1988—1989)							1.10	0.27	4.1
Mean flux (excluding April 1990)							1.19	0.38	3.1
Mean flux (April 1990 only)							0.27	0.18	1.5
Mean flux (December 1990)							1.33	0.56	2.4

that the shape of the profiles is partly due to the deposition of new, N-deficient organic sediments whose initial biological demand for N was so high that NH_4^+ release and accumulation in the pore-water and transport to the overlying water was reduced for several weeks after the flood. As will be seen below, this latter mechanism appears to have been important.

It is noteworthy that the NH_4^+ fluxes and profiles observed 10 months after the exceptional January-February 1990 flood are comparable to those found before. During the flood, water completely submerged the area shown in Fig. 2 and surface currents of the order of 10—20 $cm.s^{-1}$ were observed for several days in the ponds, which become preferential flow channels when the water-level is changing rapidly. The fact that nutrient regeneration recovered 10 months after the flood indicates that even a flood of such magnitude is insufficient scour the labile organic sediments of the pond. The two pre-flood and single post-flood sediment cores taken at the same site suggest that total C and total N increased after the flood (Fig. 7), and that new allochthonous organic matter had been deposited into the ponds. The lack of replication provides only weak evidence, however. Total C in the sediments of P. San Nicolas is within the range (3—16%) reported by Devol et al. (1984) for two Amazon floodplain lakes.

The observation that NH_4^+ fluxes measured before and 10 mo after the flood are similar imply comparable NH_4^+ regeneration rates in the sediment column. This observation can be used to verify, qualitatively, whether the unusual April 1990 profiles are due to the relaxation of pore-water NH_4^+ after a major disturbance of the upper 10 cm, or if additional biological demand is involved. Indeed, if porosity, NH_4^+ regeneration rate (R, μmol per cm^3 of sediment per day) and adsorption coefficient (K) are known, non-steady-state diagenetic modeling can be used to predict the evolution of the pore-water profiles. If we assume that R and ϕ are constant with depth, the rate of change in pore-water NH_4^+ concentration (C) is given by (Berner 1980):

$$\frac{dC}{dt} = \left(\frac{D_s}{1+K}\right)\left(\frac{d^2C}{dx^2}\right) + \left(\frac{1}{1+K}\right)\left(\frac{R}{\phi}\right) \tag{2}$$

where:

$$K = \frac{1-\phi}{\phi}\, sK' \tag{3}$$

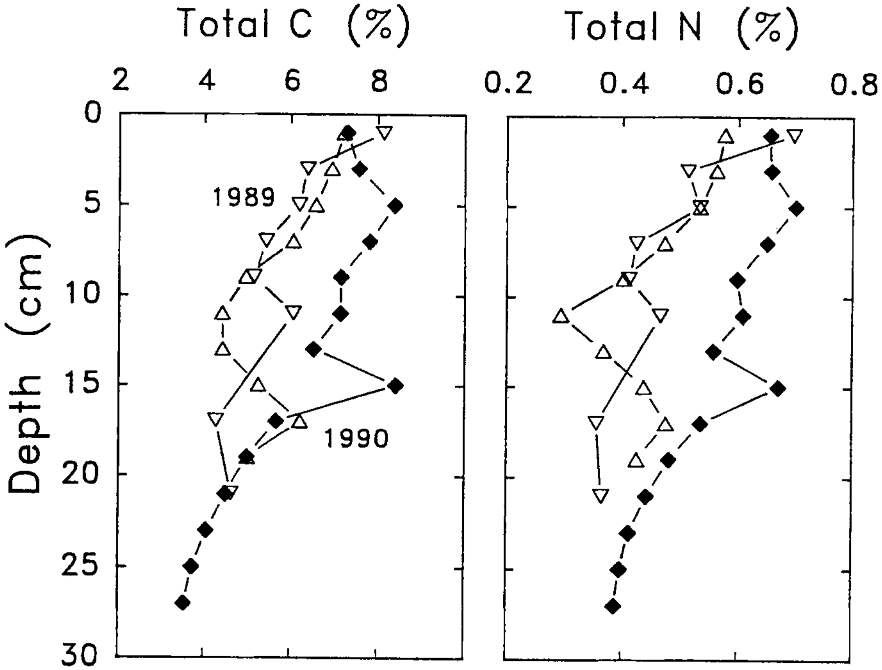

Fig. 7. Total sediment carbon and nitrogen vs. depth before (January 1989, open symbols) and after the flood (April 1990, filled symbols) in Pond San Nicolas North.

K' is the linear adsorption coefficient of NH_4^+ (liter.g^{-1}), and s is the density of solids. Eq. (2) was integrated numerically by finite difference between $t = 0$ and $t = 100$ d using a Crank-Nicolson algorithm (Gerald & Wheatley 1984) with the following assumptions and boundary conditions. R was assumed to be constant with time and distributed homogeneously in the upper 10 cm, and its integrated value set equal to the diffusive flux observed at the interface on December 1990 (this is a minimum estimate since an important proportion of the labile organic matter deposited during the flood may have decayed). K' (0.020 liter.g^{-1}) was measured by centrifugation of a 0—10 cm bulk sample followed by extraction of the pellet with 2N KCl for 2 h and measurement of NH_4^+ in both extracts. Initial and boundary conditions are:

$t = 0, x < 10\,\text{cm}: C = 0$
$t = 0, x >= 10$ cm: $C(x, 0) = 0.52(1 - \exp(-0.156x))$, ($\mu$mol.cm^{-3}), $r^2 = 0.99$, the non-linear least-squares fit of the December 1988 profiles.
$x = 0, C(x, t) = 0$

Time-dependent solution of $C(x, t)$ show that the NH_4^+ profile should regain a convex-upwards shape within 10—15 d following the flood (Fig. 8). Therefore, a model assuming positive R and simple abiotic adsorption cannot explain the persistence of a concave profile after 60 days. An additional strong NH_4^+ sink must have been present in the upper 5—10 cm of the sediments. This conclusion is consistent with the rapid disappearance of DIN in the ponds shortly after their hydrologic isolation (see below).

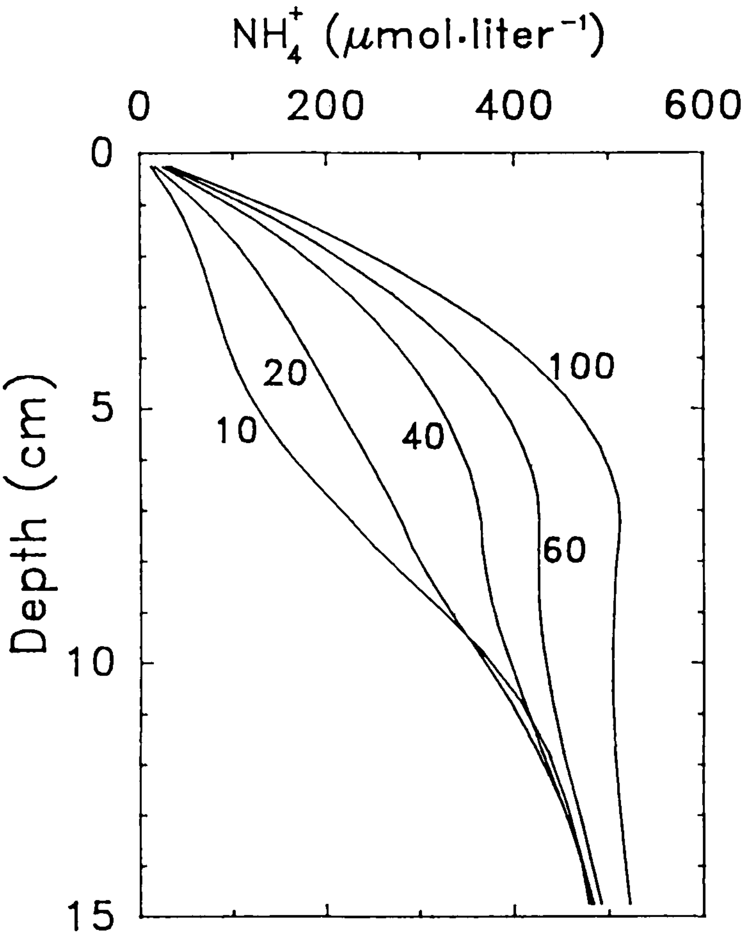

Fig. 8. Theoretical relaxation of pore-water NH_4^+ during the first 10—100 days after a flood-induced erosion of the upper 10 cm of the sediments followed by the sudden deposition of 10 cm of new sediments in Pond San Nicolas North. The model assumes that NH_4^+ production, diffusion and adsorption are the only important reactions.

Heterotrophic N_2 fixation

Heterotrophic nitrogen fixation is primarily associated with decaying litter in these systems, and appears to be strongly inhibited by DIN (Table 3). The molar ratio of ethylene formed to N_2 fixed varied considerably, from 4.3:1 to 22.6:1, among the 12 litter samples on which both measurements were made. The average C_2H_2:N_2, calculated as the sum of C_2H_2 produced divided by the sum of N_2 fixed in all experiments was 8.0:1, which is significantly higher than the 3:1 value often used to convert acetylene reduction to N_2 fixation rates. However, linear regression of C_2H_2 produced against N_2 fixed gives:

$$C_2H_4 = 3.82 \pm 1.2\ {}^{15}N_2 + 12.66 \pm 4.5, r_2 = 0.50; n = 12; \tag{4}$$

with both slope and intercept significantly different from zero ($p < 0.01$). The slope is thus close to 3:1 ratio, and lower than the 10:1 to 100:1 values reported for heterotrophic fixation in the sediments of Narragansett Bay (Seitzinger & Garber 1987). Ethylene production in samples to which no acetylene was added was insignificant. Thus, we interpret the significant positive intercept as an indication that some acetylene reduction was also mediated by non-nitrogen-fixing organisms. These results provide further caution against the use of the acetylene reduction assay of heterotrophic N_2 fixation. Eq. (4) was used to convert C_2H_4 production to N_2 fixation for dates or samples for which only acetylene reduction rates are available (Table 3). In January 1991, individual N_2 fixation rates varied considerably, from 0.32 to 7.72 μmol.g^{-1}.d^{-1}. We presume that variability in both the ratio of C_2H_4 produced to N_2 fixed and fixation rate is attributable to the heterogenous nature of the litter samples assayed.

Few values of N_2 fixation by heterotrophs associated with decaying aquatic vegetation in natural systems have been reported in the literature. Our average rates of 1.99 and 3.18 μmol.g^{-1}.d^{-1} found under low to undetectable DIN concentrations in April 1990 and January 1991 are 2—10 times higher than those found by Dierberg & Brezonik (1981) in a cypress dome swamp, and, to our knowledge, are the highest reported so far. The high N-demand by decaying vegetation is also apparent from the rapid decreases of inorganic N in the experimental vessels during incubation (Table 3). Fixation is undetectable in the open water, where cyanobacteria are normally a very minor component of the phytoplankton, but reaches the appreciable level of 0.07 μmol. liter^{-1}.d^{-1} in surface water collected in the floating meadow. Roots fixed relatively little N_2 (0.03—1.23 μmol.g^{-1}.d^{-1}) and most of it may have been associated with fine litter caught in the roots.

Table 3. Heterotrophic N_2 fixation rates ($\pm$SE) associated with litter, roots, meadow-water and open water in the ponds under various temperatures and initial (t_0) and final (t_f) DIN concentrations. The rates were either measured as ^{15}N incorporation, or calculated from acetylene reduction rates (Eq. (4), see text), and are reported on a dry weight basis.

Date	Location	Type	Temperature (°C)	$NH_4^+ + NO_3^-$ (μmol.liter^{-1})		Rate ($\mu molN_2.g^{-1}.d^{-1}$)	n
				t_0	t_f		
Apr 1990	P. San Nicolas	litter	22.5	13.6	4.6	0.37 ± 0.14	4
Apr 1990	P. San Nicolas	roots	22.5	13.6	20.5	0.17 ± 0.08	4
Apr 1990	outside tank	litter	21.0	1.1	<0.05	1.99 ± 0.58	3
Apr 1990	outside tank	roots	21.0	1.1	0.8	<0.03	3
Jan 1991	P. Baltazar	litter	29.3—31.9	<0.05	<0.05	3.18 ± 0.47	18
Jan 1991	P. Baltazar	roots	31.9	<0.05	<0.05	0.54 ± 0.19	6
Jan 1991	P. Baltazar	meadow water	31.2	<0.05	<0.05	0.07 ± 0.01[1]	2
Jan 1991	P. Baltazar	open water	31.9	<0.05	<0.05	<0.02[1]	2

[1] Rates for water samples are in $\mu molN_2.liter.d^{-1}$

The low DIN concentrations and high rates of N_2 fixation observed in the *E. crassipes* meadow may be due to the remarkably low total N (0.39 to 1.40%, $\bar{x} = 0.98\%$, Carignan et al. 1992) and high C:N ratio (30:1 to 100:1) found in the green parts of this plant during summer conditions. These values are two to three times lower than usually reported for other emergent or floating macrophytes. The development of a saprophytic microbial community capable of breaking down litter material having such a high C:N ratio likely necessitates an external source of N. The large quantity of N fixed by the decomposing litter is most probably transferred to the macrophytes since bacteria are short-lived and DIN does not accumulate in the surrounding water. Transfer of fixed N to the macrophytes may be mediated by NH_4^+ excretion from the numerous scrapers and detritivores (fish, gastropods, insects) which exploit the microbial community attached to the litter and roots of *E. crassipes*.

We have no data for autotrophic N fixation in these waterbodies. Repeated phytoplankton counts during 1989—1992 in the open waters of the north and south segments of ponds San Nicolas, Baltazar and Puente gave only traces of heterocystic cyanobacteria (Carignan & Planas, unpubl.), even in those ponds where DIN is generally undetectable. However, in Pond Baltazar only, an heterocystic *Anabaena* has been observed growing on superficial roots, and forming small scums at the border of floating meadows. Epiphytic algae became visually undetectable inside the meadows.

Denitrification

Initial NO_3^- concentration in the experimental vessels was low (0.4 μmol.liter^{-1}), but higher than the usually undetectable values found in undisturbed meadows (Carignan et al. 1992). The rate of denitrification under ambient NO_3^- was below our detection limit of 0.1 mmol.m^{-2}.d^{-1}, which supports the suggestion (Bowden 1987), that denitrification losses are relatively small in freshwater wetlands. Nitrate rapidly disappeared, however, when it concentration was raised to 98 μmol.liter^{-1}. After 16 h, 36% of the added NO_3^--N had been transformed to N_2O, 11% still remained as NO_3^-, and 53% was unaccounted for. Part of the missing N may have been taken up by macrophytes and microbes, or reduced to NH_4^+ (see below). These results indicate that a potentially significant proportion of the river-derived NO_3^- entering the ponds could be denitrified during floods.

Matching N demand and supply: Does productivity depend on external river inputs, or are the ponds self-sustained?

For reasons that are not yet well understood, the ponds of the Paraná floodplain sustain variable biomasses of floating macrophytes. Compared to the Amazon or the Orinoco, floating meadows appear to be more developed in the Paraná floodplain ponds. Pond San Nicolas and other surrounding ponds of similar size and shape in our study area normally develop a 40—100% floating macrophyte cover during prolonged (6—18 months) low water conditions. In contrast, floating macrophytes may be largely absent at low water in the ponds of the Amazon and Orinoco, and may develop a 5—50% cover during rising and high water (Junk 1970; Tundisi & Tundisi 1984; Hamilton & Lewis 1987). *E. crassipes* meadows are common in the Orinoco, but they rarely cover more than 10% of the surface. Although meadow formation is more pronounced in the Paraná, areal dry mass production is comparable in the three systems. Neiff & Poi de Neiff (1984) and Neiff (in Bonetto et al. 1984) have measured average seasonal biomass increments of 1.3—2.1 $t.ha^{-1}.mo^{-1}$ (dry weight) in nearby ponds dominated by *E. crassipes*. These values are similar to the 1.0—3.3 $t.ha^{-1}.mo^{-1}$ reported for floating *Paspalum repens* meadows in the Amazon floodplain (Junk 1970; Junk & Howard-Williams 1984).

The high production rates observed in floodplains are generally attributed to abundant nutrient supply from the main channel of the river during floods. In lakes and ponds of the floodplain, however, floods may have two opposite effects. According to the "flood pulse" hypothesis (Junk et al. 1989), high biological productivity can be sustained by the interception of river-derived nutrients. On the other hand, the large nutrient reserves present in the living and dead biomass of floating meadows and underlying organic sediments may be washed out of the ponds during floods; the extent of organic matter loss during floods may depend on factors such flood amplitude and frequency, current speeds and the presence of surrounding terrestrial vegetation barriers. Ideally, a positive or negative effect of floods on pond productivity could be shown by relating changes in macrophyte biomass to nutrient influxes from the river in representative water bodies during a representative flood. This may, however, prove exceedingly difficult to accomplish in our study site, where indirect and diffuse hydrologic connections to the main channel are common, where sheet-flow can occur, and where floods are quite unpredictable.

Indication that large external nutrient influxes from the river channel are not necessary to sustain high macrophyte net growth rates is provided by net increments in dry biomass of 1.4—1.8 $t.ha^{-1}.mo^{-1}$ recorded by Neiff & Poi de Neiff (1984) during low water phases in September—March of 1976 and 1977. As will be shown below, this observation is fully supported by estimates of internal and atmospherically-derived nutrient fluxes in the ponds. Nitrogen is clearly the element of interest here because plants cannot store large reserves of N, and because very low (this study) and limiting (Carignan et al. 1992) DIN concentrations are observed during the growth season.

We have constructed an approximate and obviously incomplete nitrogen budget (Table 4) for a 7-mo (September to March) growth period showing estimated N demand and sources for this type of system. The values are based on the following observations and assumptions. The total N demand (5.54 $mmol.m^{-2}.d^{-1}$) is the sum of N required for seasonal increase in areal biomass ($g.m^{-2}$) and surface (m^2) occupied by the meadow. Nitrogen demand due to areal dry biomass increment is taken from the average value of 5.57 $g.m^{-2}.d^{-1}$ reported in Neiff & Poi de Neiff (1984) and Bonetto et al. (1984) multiplied by the average TN content (roots + green parts, dry weight basis) of 0.98% ± 0.14 ($\bar{x}$ ± SE) measured on 25 *E. crassipes* specimens collected in 1988—1990 in San Nicolas and adjacent similar ponds during low water phases. This biomass increment is similar to the January 1990 value of 8 $g.m^{-2}.d^{-1}$ experimentally found at peak growth in control limnocorrals in San Nicolas N (Carignan et al. 1992). During the growth season, meadows of *E. crassipes* may also increase in area; actual increments may vary between 5 and 50%, depending on the surface of open water available for colonization and, presumably, on nutrient availability. We have taken a 25% increase in cover as representative of average conditions, and used a typical summer dry biomass of 2 $kg.m^{-2}$ (Neiff & Poi de Neiff 1984) with a TN content of 1% to estimate the corresponding N demand. DIN supply from precipitation at Corrientes (13.6 $mmol.m^{-2}.y^{-1}$) is taken from Pedroso & Bonetto (1985—1986). Nitrogen recycling from litter decay is based on the 1.3 $g.m^{-2}.d^{-1}$ net seasonal (September to March) decline in litter biomass reported in Neiff & Poi de Neiff (1984) and on an average TN content of 1.08% ± 0.05 measured on 26 liter samples collected in April and January. Nitrogen release from the sediments is taken from the pre-flood values of Table 2. Nitrogen fixation associated with the litter is calculated from the average of values measured at 22 and 30 °C under low DIN concentrations (Table 3) and an average summertime submerged litter biomass value of 280 $g.m^{-2}$ (Neiff & Poi de Neiff 1984). Nitrogen fixation associated with the roots is calculated from a root biomass of 600 $g.m^{-2}$ (Neiff & Poi de Neiff 1984) and values of Table 3. Finally, in the absence of relevant information, we assume that heterotrophic nitrogen fixation in

Table 4. Tentative seasonal (September to March) nitrogen budget for a floating *E. crassipes* meadow in the Paraná floodplain.

Demand	($mmolN.m^{-2}.d^{-1}$)	
Areal biomass accumulation	3.90	
Increase in meadow surface	1.64	
Total	5.54	
Supply		(%)
Litter decay	1.00	23.2
Release from sediments	1.10	25.5
N_2 fixation in litter	1.45	33.6
N_2 fixation in roots	0.65	15.1
N_2 fixation in water	0.07	1.6
Precipitation	0.04	1.0
Total	4.31	100.0

the water column is limited to the upper 50 cm normally occupied by the roots, and that autotrophic fixation is negligible.

Some of the values in Table 4 are only crude estimates. In particular, it is assumed that N supply from decaying litter and transfer of fixed N_2 to the macrophytes, presumably via bacterial turnover and animal excretion, are 100% efficient. Seasonal increase in plant cover is also variable from pond to pond. Nevertheless, the N budget indicates that the sum of internal recycling (decaying litter, flux from sediments) and N_2 fixation are within 25% of the estimated N demand by these systems. If extrapolated to a 7 mo period of low inorganic N availability and expressed on an annual basis, our N_2 fixation estimate (2.17 $mmol.m^{-2}.d^{-1}$ = 0.46 $mol.m^{-2}.y^{-1}$) would be among the highest proposed so far for freshwater wetland ecosystems (Howarth et al. 1988). When the N_2 fixation rates obtained at 29.3—31.9 °C in January 1991 are used, total fixation amounts to 2.88 $mmol.m^{-2}.d^{-1}$. This high value appears realistic since it confirms the 4.29 $mmol.m^{-2}.d^{-1}$ rate independently deduced from N budgets in limnocorral experiments conducted at 30 °C in P. San Nicolas (Carignan et al. 1992). Thus, we can conclude that high floating macrophyte productivity in this type of pond can possibly be self-sustained for long periods of time without external N inputs from the river. In other words, if a pond could be experimentally cut from river influences, it could develop a complete floating macrophyte cover and, eventually, proceed to more mature successional stages.

Nutrient dynamics during and after throughflow

At our study site, low water conditions, when they occur during the warm season, are characterized by an abundance of floating macrophytes, excess DRP, and a tight coupling between N regeneration, fixation, and uptake reactions leading to pronounced DIN depletion under plant meadows (≈ 1 μmol.liter^{-1}) and in open areas (<0.05 μmol.liter^{-1}). These conditions change radically during periods of high water, but in ways that are not entirely comparable to what has been observed for the Amazon and the Orinoco. The early 1990 flood was unusually brief and pronounced. Water rose rapidly in January 1990 and began to enter P. San Nicolas S on January 12—13, when the river reached the 4.8 m datum at Puerto Corrientes (Fig. 9). It entered San Nicolas N on January 18 at 5.4 m, and flowed through both ponds in a SW—NE direction (opposite to that of the river) for 3 d. Flow reversal occured on January 22, when the water-level reached about 6.3 m. By January 26 the level had reached 7.2 m, and the entire area shown in Fig. 2 was covered with 1—3 m of water flowing slowly in a direction parallel to that of the main channel. Water-level reached a maximum of 7.93 m on February 1, and the ponds remained connected to the River until February 14. In the last 90 y for which records are available, floods of that intensity have not occurred more than once every 5—10 years, on average. During this event, most ponds in the study area lost 80—95% their floating meadows to the surrounding fields and forests.

The evolution of DIN, DRP, water-level and water origin (Fig. 9) was similar in the six ponds during the 100 d period spanning from the end of the low water phase in January to the end of April. Thus, only the results from P. San Nicolas N are reported here. The highly dynamic behavior of DIN has been separated into three phases. Phase I corresponds to the throughflow period, during which DIN becomes abundant. DIN then becomes undetectable again during phase II, which begins immediately after hydrologic isolation, and reappears later (phase III).

Throughflow (phase I)

Ammonium remained low (0—2 μmol.liter^{-1}) during the first few days of the flood, when water was flowing through the ponds, under the meadows. It rose progressively once sheet-flow was established and reached a maximum of 7.5 μmol.liter^{-1} at the end of the flood. Nitrate initially reached 3 μmol.liter^{-1} and declined to ≈ 2 μmol.liter^{-1} for the remainder of the flood. During that time, NH_4^+ remained low (0.1—0.4 μmol.liter^{-1}) in the main channel, and NO_3^- varied between 15 and 20 μmol.liter^{-1}. Ingression

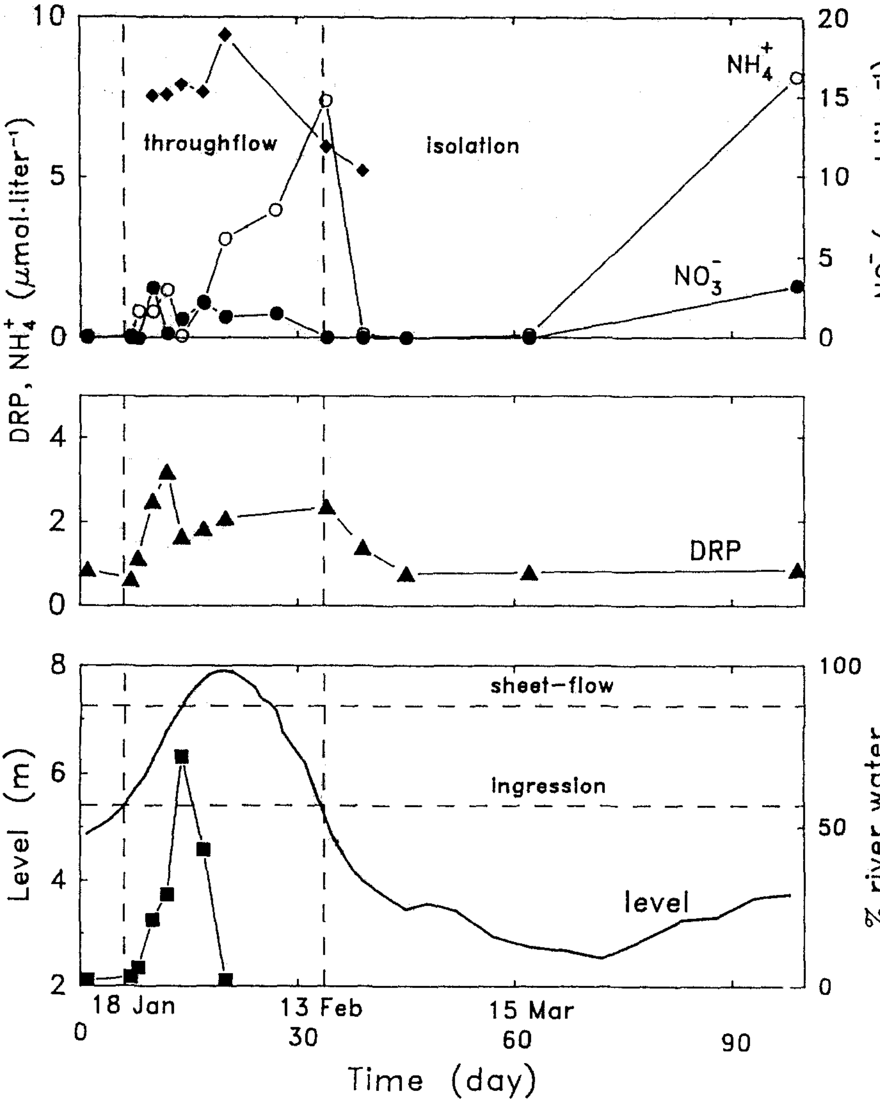

Fig. 9. Evolution of NH_4^+ (open circles), NO_3^- (filled circles), DRP (filled triangles), water-level and proportion of the water coming from the Upper Paraná (filled squares) before, during and after the January–February 1990 flood. Nitrate levels in the River are also shown (filled diamonds).

of nutrient-rich river water in the floodplain is often invoked to explain the nutrient and productivity pulse in floodplains during high waters. In our case, however, connections of the ponds with the main channel are rather indirect, and increasing DIN concentrations in the ponds do not necessarily imply that it is being imported from the river. DIN could also originate from the mineralization and nitrification of organic-N that is autochthonous to the floodplain, i.e. terrestrial N, or N originating from other upstream ponds, marshes and lakes.

Water origin was traced using dissolved Na and Ca (Fig. 10) measured in San Nicolas N (point "a" in Fig. 2), 2.3 km from the shore at low water, and in the Paraná (≈200 m from the west bank) and Paraguay rivers. During the first three days of the flood, when flow direction was opposite to that of the main channel, the Na-Ca composition of the floodplain water moved to the line joining the Paraná-Paraguay points, indicating that the water initially entering the floodplain at our study site was 1:2 mixture

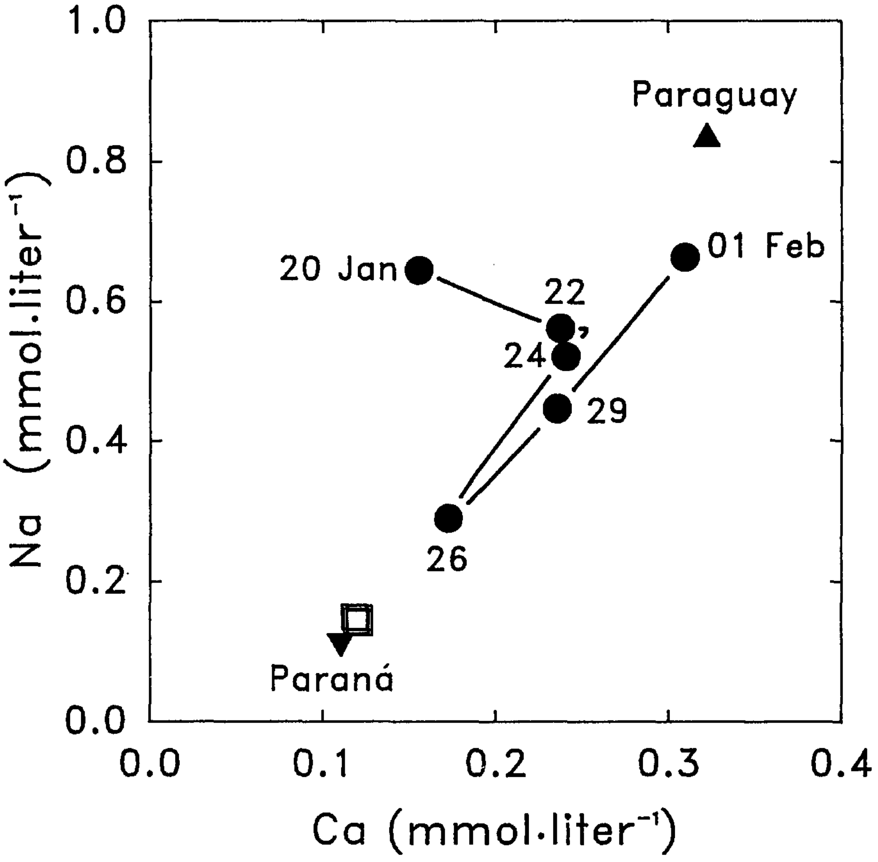

Fig. 10. Dissolved Na vs Ca in Pond San Nicolas North (filled circles) and the Paraná River (open squares) between January 20 and February 1, 1990. The mean composition of the Paraguay (filled triangle) and Upper Paraná (inversed filled triangle) reported for 1968—69 by Bonetto and Lancelle (1981) are also shown.

of Upper Paraná and Paraguay waters. Ca-Na concentrations then approached very briefly (2—3 d) the composition of the Upper Paraná River, after which they moved towards higher values typical of Paraguay River. Water from the Upper Paraná arried 2 d earlier at the level of Pond Puente, which lies 0.7 km closer to the main channel. Water from the Paraguay, however, reached both sites simultaneously. Waters of the Paraguay and Upper Paraná rivers are usually well separated at the level of Corrientes. We speculate that the short incursion of Upper Paraná water into the floodplain is due to the fact that the rising waters of the Upper Paraná may have temporarily dammed the Paraguay, which then spilled in its own floodplain for a few days. Paraguay water then began to move in a S-W direction through the connecting Paraná floodplain and reached stations "a", "c" and "d" simultaneously on January 29.

During this time interval, two types of waters were visually distinguishable in the floodplain: white low-oxygen (2—3 ppm O_2), turbid (Secchi = 20—40 cm) waters, and humic-colored, deoxygenated (0—1 ppm), less turbid (Secchi = 40—60 cm) waters. Areal reconnaissance showed that almost no mixing took place between white and dark waters as the transition between the two was very sharp (1—10 m). Between January 10 and 26, the white waters successively reached ponds c, d and a—b (Fig. 2). Sheet-flow conditions were established around January 27, and at peak flood, on February 1, the white/dark waters front was located about 4 km from the main channel.

We used the large difference in Na concentration between floodplain and Upper Paraná water, and assumed conservative mixing to estimate the relative contribution of Upper Paraná water at the level of P. San Nicolas as (Forsberg et al. 1988):

$$F = 100\,[(\mathrm{Na}_r - \mathrm{Na}_p)/(\mathrm{Na}_r - 675)]$$

where Na_r is the Na concentration in the Upper Paraná, Na_p is the Na concentration in the pond, and 675 is the average Na concentration (μmol.liter^{-1}) found in the ponds before the flood, taken as representative of floodplain water. The results (Fig. 9, lower panel) show that the proportion of water originating from the Upper Paraná reached a maximum of 72% on January 26. The proportion of Upper Paraná water may be underestimated by ≈ 15% because because a third endmember (Paraguay) with a higher Na concentration (850 μmol.liter^{-1}) than that of the floodplain was involved. Nevertheless, the results indicate that the NO_3^- appearing at the sampling site during the flood has a riverine origin. Nitrate concentrations were, however, much lower than those expected from the mixing proportions of floodplain and river water. On January 26 for example, 1.2 μmol.liter^{-1} of NO_3^- was observed at site "a" compared to the 11.5 value expected from a 72:28 mixture of Upper Paraná water (NO_3^- = 16 μmol.liter^{-1}) and floodplain water (undertectable NO_3^-). Nitrate remained low after January 29, when the water from the Paraguay (NO_3^- = 19 μmol.liter^{-1}, Bonetto & Lancelle 1981) became dominant. Thus, >90% of the river NO_3^- had been taken up or transformed by the time it reached our site.

The initial decrease in NO_3^- concentration in river-water as it flows through the floodplain may be due to several reactions including uptake by aquatic plants and micro-organisms, denitrification and dissimilatory reduction to NH_4^+. Uptake by floating macrophytes may have been important at the beginning of the flood, when NO_3^--rich river-water was slowly (5—10 m^3.s^{-1}) channeled through the ponds under the macrophyte meadows. Denitrification in the anoxic or near-anoxic conditions prevailing in the root mat may have also been important at this stage. Once sheet-flow was established, however, NO_3^- uptake by floating macrophytes must have become negligible because they represent a relatively minor component (5—10%) of the total floodplain area. During sheet-flow, NO_3^- may have been lost by denitrification or dissimilatory reduction to NH_4^+ in the poorly oxygenated water and soil/water interface. Nitrate uptake by phytoplankton and microbial heterotrophs can probably be ruled out because of unfavorable turbulence and light conditions, and because the sheet-flow period coincided with the appearance of high NH_4^+ concentrations in the waters, which is a preferred source of N for most algae and bacteria.

The origin of the increasing NH_4^+ is somewhat uncertain. It cannot have been imported as such from the river since NH_4^+ never exceeded 0.4 μmol.liter^{-1} in the main channel before and during the flood. The three remaining possibilities are loss of exchangeable NH_4^+ from floodplain soils, mineralization of organic-N in the floodplain, and dissimilatory reduction of river-derived NO_3^- in the suboxic floodplain environment. During sheet-flow conditions, white NO_3^--rich river-water never reached points "e" and "f" on Fig. 2. If the mineralization of organic-N from decaying vegetation and litter or NH_4^+ desorption from soils had been an important source of NH_4^+, it should have been observed in both dark and white waters. Yet, NH_4^+ (and NO_3^-) remained undetectable or lower than 0.3 μmol.liter^{-1} in the dark waters of stations "e" and "f". Thus, dissimilatory reduction of NO_3^- to NH_4^+ may have been important. This reaction has been observed in other oxygen-depleted environments including seawater (Samuelsson 1985), marine sediments (Enoksson & Samuelsson 1987), marshes (Hemond 1983; Bowden 1984) and soils (Buresh & Patrick

1978). The importance of this reaction deserves further study in the floodplain environment.

Early isolation (phase II)

The early isolation of ponds (phase II) is characterized by an immediate decrease in DIN to undetectable levels (Fig. 9). DIN demand by macrophytes was then negligible since ≈ 95% of the plants had been lost. Rapid phytoplankton growth could explain the initial DIN depletion, but cannot explain why DIN remained undetectable during at least 25 d. Chlorophyll-*a* was not measured at the time; we have found since that it can reach 25 μg.liter^{-1} in some of these ponds. Assuming a N:chlorophyll-*a* ratio of ≈ 0.5 μmol.μg^{-1} in phytoplankton, the new production of 25 μg of chlorophyll-*a* would require approximately 12.5 μmol of DIN, a value which is consistent with the rapid initial DIN decrease of 8 μmol.liter^{-1} in the pond. If NH_4^+ flux from the sediment (1.2 mmol.m^{-2}.d^{-1}) had not been perturbed by the deposition of N-deficient material, DIN should have begun to increase again at a rate of approximately 0.6 μmol.liter^{-1}.d^{-1}, given a mean depth of 2 m, soon after the establishment of a stable phytoplankton population. The prolonged absence of DIN in the ponds supports the hypothesis that a strong sedimentary DIN sink (allochthonous N-deficient organic matter) persisted for some time after hydrologic isolation.

Late isolation (phase III)

Ammonium and NO_3^- began to increase sometime between 30 and 60 d following isolation. By April 22, 1990, DIN had reached 11.2 μmol.liter^{-1} in P. San Nicolas N (Fig. 9). Floating macrophytes had not yet significantly recovered at that time (Pond San Nicolas N. had only developed a ≈ 15% cover by January 1991). The most likely cause for the increase in DIN is the re-establishment of a substantial NH_4^+ flux from the sediment ($\bar{x}$ = 0.27 ± 0.11 mmol.m^{-2}.d^{-1} on April 30, Table 2), and absence of significant net demand by the biota after mid-March. This scenario implies that litter decomposition, previously invoked to explain prolonged DIN depletion, ceased to serve as a net DIN sink after mid-March. On April 22, 1990, we measured NO_3^- concentrations of 3.2, 5.2, 0.33, 0.04, 2.4 and 3.3 μmol.liter^{-1} in ponds San Nicolas N, S, Baltazar-N, -S, Puente-N and -S, respectively. Because NO_3^- concentrations in the ponds were relatively high, loss of DIN by denitrification, especially during stratification events, may have been significant at that time.

Phosphorus

The omnipresence of substantial amounts of DRP in the floodplain, regardless of biological demand and redox conditions, contrasts with what is observed in most freshwater environments, where it is often undetectable, or strongly influenced by biological requirements. Dissolved reactive phosphorus increased to 2—3 μmol.liter^{-1} during throughflow (Fig. 9), possibly as a result of low dissolved oxygen concentrations in the floodplain and/or mineralization of organic-P. The most striking aspect of the evolution of DRP is its contrasting behavior with that of DIN after isolation. While DIN concentrations became undetectable shortly after isolation and increased after 25 d, DRP merely decreased to pre-flood levels and remained constant afterward. Thus, DRP concentrations seem largely unaffected by periods of high or low biological demand, which indicates the presence of high-capacity buffer mechanisms (see Froelich 1988) in the ponds.

In the Amazon and Orinoco floodplains, DRP concentrations of 0.2—1 μmol.liter^{-1} are common in lakes which receive alluvion-rich "white waters", and which are not rapidly flushed with local drainage water (Forsberg et al. 1988; Hamilton & Lewis 1990). Nevertheless, DRP may temporarily decrease below 0.1 μmol.liter^{-1} at low water in these lakes. In the Paraná floodplain, the relatively high abundance of P may be due to the high suspended load of the Paraguay River which directly influences the floodplain at our study site. Pedroso & Bonetto (1988) have reported a mean TP concentration of 1.5 μmol.liter^{-1} for Upper Paraná water. Unfortunately, total P data for the Paraguay River at its confluence with the Paraná are not available, but on 22 January 1990, we measured TP concentrations of 9.6 μmol.liter^{-1} in a water sample taken 200 m offshore from the right bank of the Paraná. Such a high value reflects the influence of the very high (20—80 μmol.liter^{-1}, Pedroso and Bonetto 1987) TP load of the Bermejo River which has an average concentration of suspended solids of 6.5 g.liter^{-1} (Drago and Amsler 1988), and flows into the Paraguay 100 km above the confluence. Water entering the ponds between January 20—22 contained 5.5—10.0 μmol.liter^{-1} of TP. These values are much higher than those reported for the white waters of the Amazon and Orinoco.

Despite the presumed importance of the river as a source of P to the ponds, the redistribution of organic and mineral P within the floodplain during high waters cannot be ruled out. Terrestrial communities can generally accumulate organic and inorganic P reserves, and the abundance of P in the ponds may simply reflect frequent transfers from terrestrial to aquatic components. These possibilities could be verified by comparative studies of the P status of the floodplain of the Paraguay River, above and below its confluence with the P-rich Bermejo River.

Impact of floods on floating meadows

The above results allow us to draw some tentative conclusions on the impact of riverine flooding on floating macrophyte cover in the Paraná. According to the flood-pulse hypothesis formulated by Junk et al. (1989) and largely inspired by observations in the Amazon, the ingression of nutrient-rich water stimulates biological production in the floodplain environment. Our observations do not support this hypothesis in the case of floating macrophytes in the Paraná floodplain, where floods are usually of lesser amplitude and of shorter duration.

During an average flood in the Paraná floodplain, water-level rises about 1.2 m above the 4.8 m ingression level (Fig. 1), which is insufficient to submerge most levées. Once the floodplain and main channel water-levels have been equilibrated, currents become negligible and the floodplain and main channel become two separate hydrologic entities. Thus, appreciable nutrient import from the main channel can occur only during rising water-level. Pond surface area may increase by 10—30% during such events. Assuming a mean NO_3^- concentration of 15 μmol.liter^{-1} in channel-water, and that none of it is denitrified, this would represent an import of 18 mmol.m^{-2} of NO_3^- for each flooding event. This quantity is smaller than the 41 mmol.m^{-2}.y^{-1} atmospheric deposition rate of nitrogen reported by Bowden (1987) for 7 wetlands. It is also nearly one hundred times smaller than the average 1.57 mol.m^{-2}.y^{-1} N-requirement of freshwater wetlands proposed by the same author, and small compared to the estimated N requirement (1.5 mol.m^{-2}.y^{-1}), fixation (0.46 mol.m^{-2}.y^{-1}) and flux from the sediment (0.43 mol.m^{-2}.y^{-1}) found in this study for the floating *E. crassipes* meadow. These considerations suggest that the gain in meadow biomass due to the increased availability of DIN during floods is likely to be more than offset by losses due to stranding during retreating waters.

During more exceptional floods, when water-level reaches or exceeds 7.2 m, sheet-flow occurs and DIN concentration increases markedly. One might then expect an increase in meadow productivity since the growth rate of *E. crassipes* is N-limited during low water. During such events, total leaf-N increases to presumably non-limiting values (2—2.5%) in *E. crassipes* and growth may be stimulated. However, sheet-flow conditions normally persist for very short periods of time (weeks) compared to months for the Amazon and the Orinoco and the plants may not have enough time to profit from these more fertile conditions. Furthermore, most meadows are lost to surrounding levée vegetation and wetlands during such floods. Although sedimentary nutrient reserves may be conserved, loss of meadows means that pronounced floods reduce total nutrient reserves and primary production in the ponds and resets them to less productive, younger successional stages.

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