The effect of prolonged floods on *Eichhornia crassipes* growth in Paraná River floodplain lakes

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ABSTRACT: The effect of prolonged floods on *Eichhornia crassipes* growth in Paraná River floodplain lakes. The growth response of *Eichhornia crassipes* was studied in two floodplain lakes with different inundation regimes and one artificial pond isolated from the Paraná River. We measured the number and the length of green leaves for 12 months to obtain leaf density, maximum leaf length and monthly size distribution frequency. We also measured the increase in leaf dry weigth for 21 days at the end of the growing season (March, 1998). In the same occasion and at the end of prolonged floods (August, 1998), water samples and green leaves subsamples were analysed to determine nutrient content. In the last years, the floodplain lakes were frequently affected by extreme floods due to El Niño events. The prolonged inundation condition in the lake that had a long lasting inundation phase (371 days) was characterized by increases in the mean maximum leaf size (up to 111 cm), increases in the modal leaf length (most prominent mode= 105 cm), high increase in biomass (25 g m^2 day^{-1}) and high nutrient content of green leaves (total nitrogen= 2.53%). The growth response was lower in the lake which had less number of flooding days per year (204) than the lake with the longest duration of the flooding. Nevertheless, it was higher than that described in a previous paper for extreme floods of short duration in the same lakes. In the artificial pond, average increase of green leaves biomass accounted to only 5 g m^2 day^{-1}. The total isolation condition was characterized by decreases in the modal leaf length of the mature plants and increases in standing dead leaves density. These results are discussed in the context of the River Pulse Concept and variation on this theme to Paraná River floodplain.

Key words: River pulses; Tropical rivers; *Eichhornia crassipes*; Plant growth; Floating meadows.

RESUMO: O efeito de inundações prolongadas sobre o crescimento de *Eichhornia crassipes* em lagoas da planície de inundação do Rio Paraná. A resposta no crescimento de *Eichhornia crassipes* foi estudada em dois lagos da planície de inundação com diferentes regimes de inundação e em uma lagoa artificial isolada do Rio Paraná. Medimos o número e o comprimento de folhas verdes durante 12 meses para obter a densidade foliar, o comprimento foliar máximo e a frequência da distribuição em tamanho mensal. Nós medimos também o incremento em peso seco foliar durante 21 dias no fim da estação de crescimento (março 1998). Na mesma ocasião e no término de inundações prolongadas (agosto 1998), em amostras de água e em subamostras de folhas verdes foi determinado o conteúdo de nutrientes. Nos últimos anos, os lagos da planície de inundação foram frequentemente afetados por inundações extremas devido aos eventos de El'Niño. A condição de inundação prolongada no lago que teve uma longa duração da fase de inundação (371 dias) foi caracterizada por aumento no tamanho foliar máximo médio (até 111 cm), aumentos no comprimento foliar da moda (moda mais proeminente =105 cm), elevado incremento em biomassa (25 g.m^2.dia^{-1}) e alto conteúdo em nutrientes das folhas verdes (nitrogênio total= 2.53%). A resposta no crescimento foi mais baixo no lago que tem número menor de dias de inundação por/ano (204) que no lago com duração mais prolongada da inundação. Contudo, foi mais alto que aquela descrita em trabalho anterior para inundações extremas de

curta duração nos mersmos lagos. Na lagoa artificial, o aumento médio de biomassa das folhas verdes foi calculado em somente 5 $g.m^{-2}.dia^{-1}$. A condição de isolamento total foi caracterizada por diminuições no comprimento foliar modal e aumentos na densidade de folhas mortas. Esses resultados são discutidos no contexto do Conceito do Pulso do Rio e na variação deste tema para a planície de inundação do Rio Paraná.

Palavras—Chave: Pulsos de Rio, rios tropicais, *Eichhornia crassipes*, crescimento vegetal, bancos flutuantes.

Introduction

The Paraná River has an irregular hydrological regime with normal and extreme floods. Extreme floods attributed to El Niño events (Nuñez & Vargas, 1998) may deeply affect the floodplain habitat. During floods, turbid river water penetrates into the floodplain across meander scroll and oxbow lakes through the gallery forest, marginal wetlands and secondary channels.

Many floodplain lakes are dominated by *Eichhornia crassipes* (Mart. Solms.) that may cover 30-100% of the available surface. Monthly average biomass ranges from 8.6 to 24 t ha^{-1} dry weight, with more than 35% as root tissue (Neiff & Poi de Neiff, 1984). Biomass increases from August to March and declines to about 50% of its annual maximum during the cool season (May to July).

According to the flood-pulse hypothesis formulated by Junk *et al.* (1989), the inflow of nutrient-rich water stimulated biological production in the floodplain environment. Carignan & Neiff (1992) found that the high water and low water phases are characterized by a very dynamic behavior of dissolved inorganic nitrogen. Compared to DIN, dissolved reactive phosphorus concentrations remain relatively high and change little during and after the flood. One might expect then, an increase in *E. crassipes* productivity after the flood since the growth rate of the plants is N-limited during low water. However, because of their short duration, floods do not appear to stimulate *E. crassipes* production in the Paraná floodplain (Carignan & Neiff, 1992).

In relation to the last hypothesis, we studied the effect of prolonged floods on the growth response (leaf length, number of leaves per m^2, increase in biomass) of *Eichhornia crassipes* in two lakes with different inundation regimes. Due to other possible factors such as temperature that affect plant growth response, comparison between the two floodplain lakes and one isolated pond not subjected to flooding was examined.

Study site

Near Corrientes city (Argentina), the Paraná River flows as a typical floodplain river. On the right margin there is a low-lying land prone to flooding and on the left margin the river is flanked by high banks (approximately 8 m high). To study the effects of floods on *Eichhornia crassipes* growth, two natural lakes (Fig. 1) located on the right margin of the Paraná River and one artificial pond, were selected.

Floodplain lakes are small (200 x 2000 m), shallow (0.4-2 m) and separated by alluvial levees (50 m wide, 1-2 m high) occupied by gallery forests.

San Nicolás lake (Site A, 27°27'S; 58°55'W) is connected to the Paraná river from one to three times per year, when the water level at Puerto Corrientes is above 4.85 m. El Puente lake (Site B, 26°26'S; 58°51'W) is more frequently inundated with long-lasting floods. In both lakes, *Eichhornia crassipes* was found in monospecific stands that cover up 70% of the water surface. Both lakes have no direct contact with the river during low water and they have a 10-30 cm thick superficial organic sediment layer that sustains internal nutrient fluxes to the water column of 20 mg m^{-2} day^{-1} for NH_4^+-N and 10 mg m^{-2} day^{-1} for PO_4-P (Carignan & Neiff, 1992).

Because lakes situated on the floodplain of the Paraná River are regularly flooded, the isolated condition was only possible in an artificial pond (1.5m depth). The pond (Site C, 27°28'S; 58°44'W) was filled with water from San.Nicolás lake and stocked with water hyacinth. Its initial chemical condition and the coverage by the plants corresponded to the floodplain lakes during low water phases.

At all three sites the growth form of water hyacinyh with elongate leaves, which occurs in dense mats, was dominant. The inflated petiole morphotype, which occurs in more open situations, was not found during the study period.
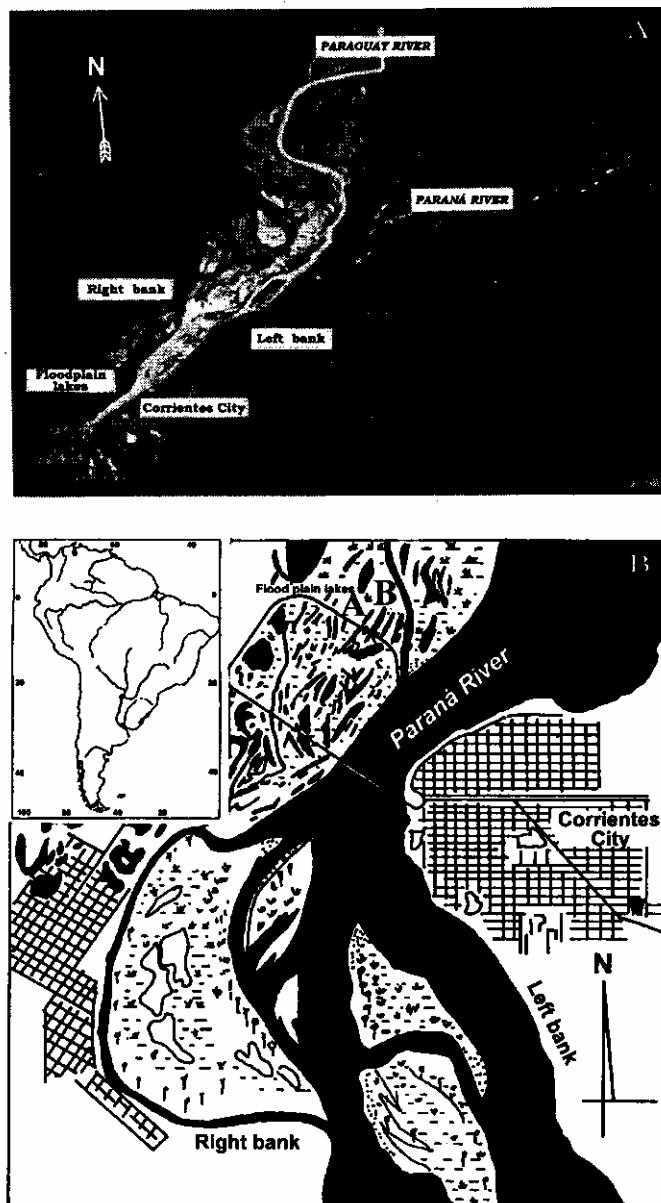

Figure 1: a) Satellite image of the confluence of the Paraná and Paraguay Rivers (scale~1:500,000). At the study sites, located 30 km downstream from the confluence, both river waters are well separated and complete mixing occurs 300 km downstream. b) Location of the sampling sites on the Paraná River floodplain.

Methods

Sampling of *Eichhornia crassipes* stands was performed at monthly intervals between March 1997 and March 1998. For each floodplain lake and for the pond, the average number of leaves was determined, in triplicate, inside a 0.30 m² circular plot from 3m of the margin. All leaves within the plot were cut off and collected in plastic bags. In the laboratory, green and standing dead leaves were separated and counted.

The length of 9405 green leaves was measured from the base of the petiole up to the end of the leaf. The monthly average of n value was 238 ± 56 (Site A), 250 ± 66 (Site B), 255 ± 55 (Site C) according to the leaf density in the plot. Length data from each month were grouped in size classes with 5 cm width intervals to obtain average monthly frequency distribution for each Site. On each sampling data the length of the longest leaf of each plot were used to calculated the mean maximum leaf length.

The significance of differences was determining using ANOVA of normalized data (logarithmic transformation). In order to relate maximum leaf size with flooding regime, Pearson correlation procedure was applied (Steel & Torrie, 1985). Flooding regime is expressed as the number of flooding days per year (Van den Brink *et al.*, 1994). At Site C the number of flooding days were considered to be zero.

During March, when the water hyacinth has its peak of biomass, the rate of increase in leaf dry weight was calculated from the change in biomass over 21 days. Green leaves harvested from the circular plot were separated, dried at 105°C and weighed.

On March 12, 1998 and August 27, 1998, integrated water column samples (1 liter) were collected within the floating meadows. Samples were filtered within 1-2 h of collection on prewashed Gelman DM-450 (0.45 µm) membranes for spectrophotometric analyses of NH_4^+ (indophenol blue method), $NO_3^- + NO_2^-$ (henceforth called NO_3^-) by reduction on Cd and total phosphorus (molybdenum blue method) after persulfate oxidation (APHA, 1995). In the same occasions, 10 green leaves from each plot were dried at 60°C to determine nutrient content. Nitrogen (macro Kjeldähl method), phosphorus (AOAC, 1990) and fiber content (Ankom Fiber Analyzer) were expressed as percentage of dry weight.

Air temperature and solar radiation were recorded with a LiCor (LI-1200S) data logger.

Results

Hydrological dynamic

The Paraná River at Corrientes city has a pulsing regime (Fig. 2) with normal floods (water level close to 6 m) and extreme floods (water level above 7 m).

A *pulse* is defined here, according to Neiff (1996), as the time between the beginning of the flooding and the end of the isolated period. Each pulse has high water phase when the river water enters the lake and low water phase when the lake remains isolated from the river.

Each floodplain lake has different inundation regimes according to their location in the geomorphological gradient, i.e. site A was connected with the main channel during 404 days (Table 1), whereas site B was flooded 520 days during the same period (October 1996-August 1998). The number of pulses was higher at site A than at site B.

In 1997, after a short exceptionally high water phase (that occurred in January) there was a prolonged low water phase (Fig. 2 and Table 1). Normal floods occurred during winter. From October 1997 through August 1998, the floodplain lakes became flooded for several months. At site B, pulse 4 had a long lasting inundation phase (283 days). At site A, the maximum duration of the high water phase was 134 days in pulse 8 (Fig. 2 and Table 1).

Insolation and temperature

Solar radiation increased gradually to a maximum of 32 MJ m⁻² day⁻¹ in December 1997 (Fig. 3). Values were considerably lower from April to September. Maximum ambient air temperature ranged from a daily average of 15° C during July 1997 to 37° C during January 1998. The winter of 1997 was extremely mild, with no temperatures below 0° C and a minimum temperature of 1.5° C. September, October and November were unusually hot, with temperatures rising to 40° C.

Table I: Duration of the low water and high water phase and number of pulses between October 1996 and August 1998

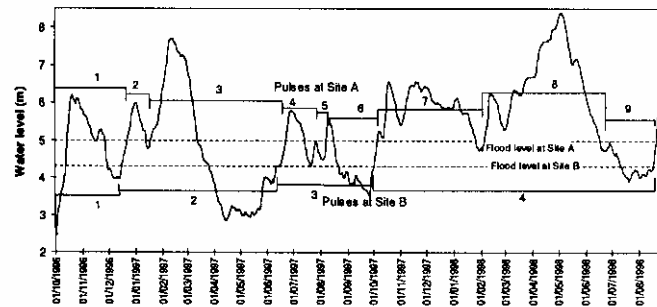| Site A					Site B				
Pulse	Start date	Time	Low water phase (days)	High water phase (days)	Pulse	Start date	Time	Low water phase (days)	High water phase (days)
1	14-Octo-96	68	25	43	1	12-Oct-96	65	16	49
2	22-Dec-96	27	5	22	2	17-Dec-96	181	81	100
3	18-Jan-97	154	98	56	3	17-Jun-97	108	20	88
4	22-Jun-97	35	12	23	4	3-Oct-97	318	35	283
5	28-Jul-97	10	9	1					
6	8-Aug-97	58	48	10					
7	6-Oct-97	121	7	114					
8	5-Feb-98	144	10	134					
9	27-Jun-98	52	51	1					

Figure 2: Water level of the Paraná river at Puerto Corrientes between October 1996 and August 1998 and number of pulses according to the flood level at each site.
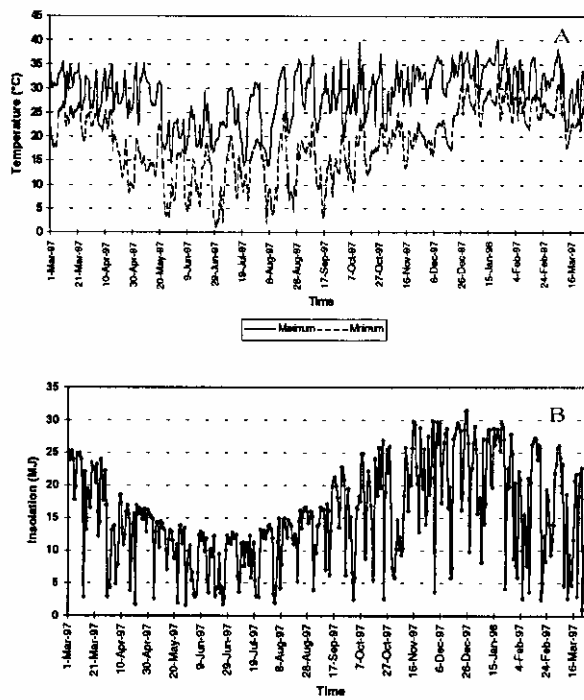

Figure 3: Daily air temperatures (A) and solar radiation (B).

Leaf density and leaf length

The mean monthly leaf densities per m² (green + standing dead leaves) are represented in Fig. 4. No significant differences were found between the number of green leaves per m² of the floodplain lakes and that of the artificial pond ($F_{2,115}$ = 1.79, P<0.01). At three sites, a relatively constant density was found. This high density maintained throughout the year was probably due to the mild winter.

There was significantly more standing dead leaves per m² ($F_{2,115}$ = 85.03, P<0.01) in the artificial pond, isolated from the main channel, than in the floodplain lakes, which were colonized by more vigorous plants (Fig. 4). At site C, the density of leaves and the proportion of standing dead leaves were similar to those of the San Nicolás lake in the low water phase of pulse 1 (leaves per m² = 550, standing dead leaves= 23 %, Casco & Poi de Neiff, 1998) when the plants grew limited by nitrogen.

The average maximum length of the green leaves was higher in the floodplain lakes than in the artificial pond (Fig. 5). At the end of the winter, the mean maximum leaf length decreased slightly in the floodplain lakes, whereas in the pond the value declined to 48 cm. Significant differences were found when ANOVA was used to compare maximum leaf length at Sites A and B ($F_{1,74}$ = 6.81, P< 0.01) and at all three Sites ($F_{1,111}$=6.21, P< 0.01).

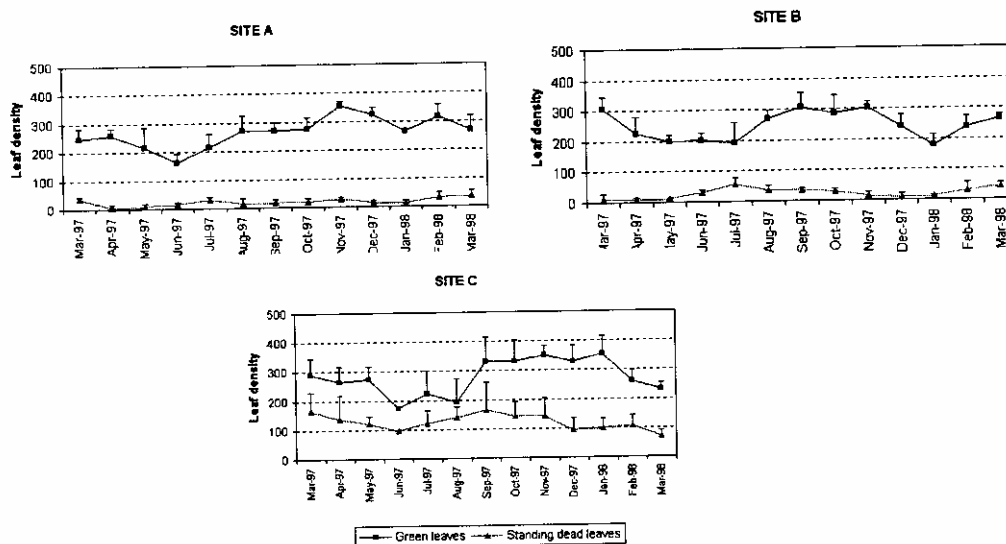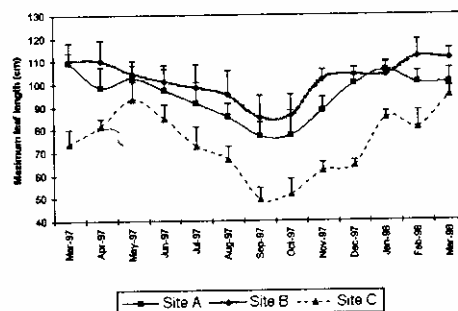Figure 4: Mean monthly leaf density ± 1 SD (n=3) of green, standing dead and wilt leaves at Sites A,B and C.

Figure 5: Mean monthly maximum leaf length ± 1 SD (n=3) at the study sites.

The leaf length data from each month were arranged in size classes to obtain average monthly frequency distributions for each site (Fig. 6). It is clear from the graphs
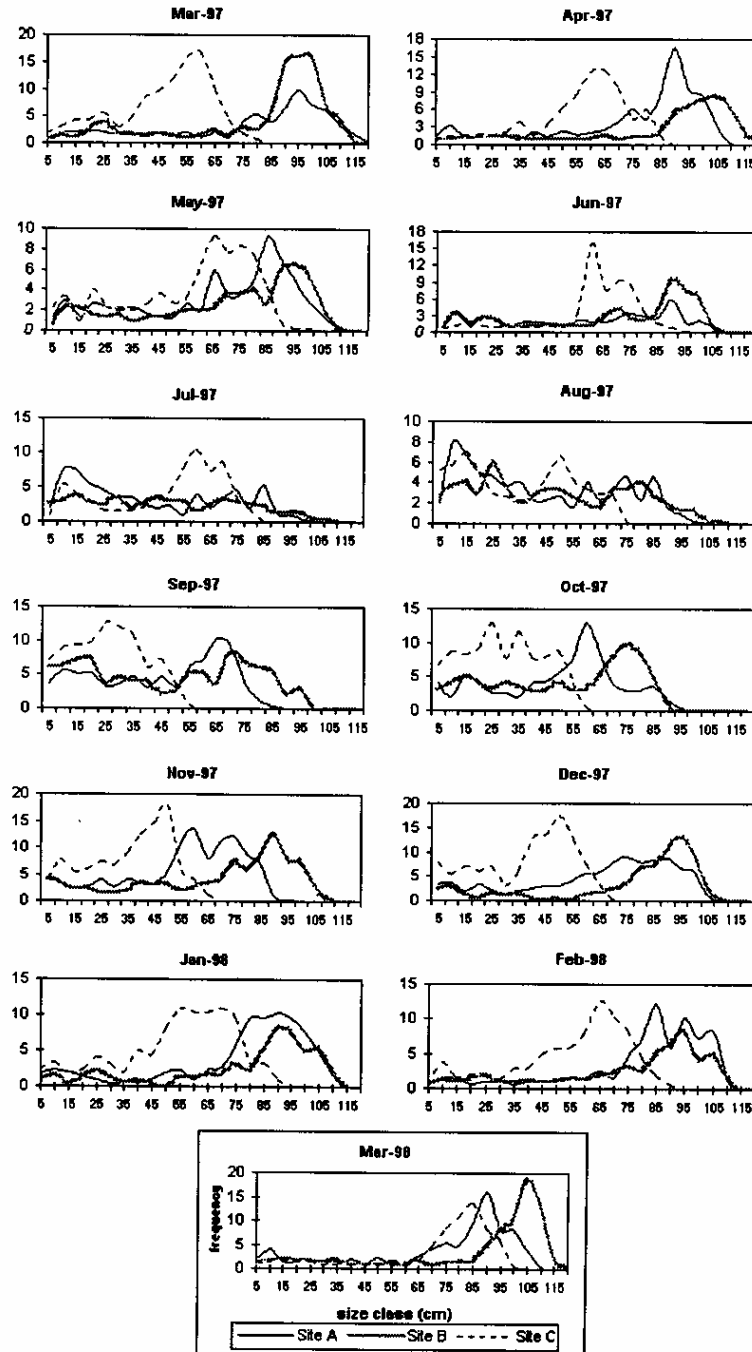

Figure 6: Mean leaf length frequency of the size class for each month at Sites A, B and C.

that leaf size distribution changed rapidly at each site during the annual cycle. In the artificial pond, the most prominent mode (65 cm) indicated the preponderance of small leaves. In the floodplain lakes, the distributions represented the abundance of large leaves which most prominent mode increased to 90 cm (Site A) and 105 cm (Site B). At the end of the winter there were broader and polymodal curves at these sites, with very little change in the frequency of the different size classes. It was due to the senescence of the larger leaves and the subsequent replacement by plants of the new growth.

Biomass and nutrient content

The increase in biomass of green leaves measured from February 11, 1998 to March 4, 1998, was highest at Site B (25 g m² day⁻¹), whereas at Site A was lower (Table II). In the artificial pond, growth was only 5 g m² day⁻¹ during the same interval (Table II).

At the end of the growth period, nitrate and ammonium concentrations in the water within the floating meadows were similar at all three sites (Table II), whereas phosphorus concentration was fifteen times higher in the floodplain lakes than in the pond. During March 1998, the green leaves had a similar concentration of nitrogen (Table II) at both study sites. At the end of the prolonged flooding (August 1998) the dissolved inorganic concentration of nitrogen increases in the floodplain lakes (Table II). Green leaves collected at this time showed a high nitrogen content specially in the lake with more prolonged inundation phase (Table II).

Table II: Average of increase in biomass, elemental concentrations of *E. crassipes* green leaves on an ash-free dry weight basis and water condition.

GREEN LEAVES	March 1998			August 1998		
	Site A	Site B	Site C	Site A	Site B	Site C
Increase in biomass (g.m².day⁻¹)	8.3	25	5	—	—	—
Total nitrogen (%)	1.58	1.338	1.44	2.13	2.53	1.61
	± 0.03	± 0.01	± 0.04	± 0.05	± 0.03	± 0.00
Protein (%)	9.94	8.40	9.02	13.37	16.01	10.10
	± 0.2	± 0.11	± 0.2	± 0.02	± 0.00	± 0.01
Total phosphorus (%)	0.27	0.243	0.13	0.35	0.23	0.10
	± 0.003	± 0.02	± 0.005	± 0.02	± 0.00	± 0.005
Acid detergent fiber	29.60	28.80	27.00	—	—	—
	± 0.35	± 0.7	± 0.3			
Lignin (%)	1.04	0.96	0.91	—	—	—
	± 0.12	± 0.06	± 0.14			
WATER CONDITION						
Water temperature (°C)	25	25	22	16.5	16.0	17.2
Dissolved oxygen (mg.l⁻¹)	1.6	2.8	1.5	5.0	5.3	2.3
Conductivity (µS.cm⁻¹)	170	190	299	210	115	251
pH	7.1	7.2	7.1	8.2	8.0	7.2
N·(NO₃+NO₂) (µg.l⁻¹)	10	bdl	<5	65	100	bdl
N-NH₄ (µg.l⁻¹)	20	45	30	60	85	35
P-PO₄ (µg.l⁻¹)	155	150	10	93	105	10
N:P	0.19	0.3	3.5	1.34	1.76	3.5

bdl = below detection limit. Values are the average ± 1 SD (n=3)

Discussion

Our results support previous studies about the importance of pulses for aquatic plant communities and demostrated a clear effect of flooding on the growth responses of *Eichhornia crassipes* .

During low water condition, low DIN:DRP ratios (0.16-1.0 m mol.liter⁻¹) and low DIN (0.5-4.8 m mol.liter⁻¹) in the root-zone of the floating meadows suggest that *E. crassipes* growth is limited by nitrogen.

During extreme floods, when water level reaches or exceeded 7 m. sheet-floods occur and DIN increased to high values 11.2 m mol.liter⁻¹ in the floodplain lakes (Carignan & Neiff, 1992). Compared to DIN, DRP concentrations remain relatively high and change little during and after the flood. However, if sheet-flow conditions persist for very short

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periods of time these plants may not have enough time to benefit from these more fertile conditions and production would not be then stimulated (Carignan & Neiff, 1992). During 1997 and 1998, long term floods due to El Niño phenomena resulted in exceptional plant growth. The prolonged inundation condition was characterized by increases in leaf size, increases in biomass values and high nutrient content in the green leaves; therefore, it differs from what was described by Carignan & Neiff (1992) for extreme floods of short duration that are the most frequent ones.

Between March 1997 and March 1998 floodplain lakes had 371 (Site B) and 204 (Site A) flooding days and the artificial pond remained isolated. The significant correlation between maximum leaf length and number of flooding days year^{-1} (r = 0.667, P < 0.01, n=118) provide support for the importance of flooding regimes.

The unusually mild winter followed by a warm spring would have been much more conductive to optimal growth in the floodplain lakes, but the differences in growth responses between these lakes and the artificial pond, isolated from the Paraná River are consistent with the pulse hypothesis.

The highest increases in biomass of *E. crassipes* (25 g m^{-2} day^{-1}) was found in the lake with the longest duration of the flooding. This value is close to the maximum absolute increase of *E. crassipes* biomass cited in the literature (Center & Spencer,1981). The nitrogen content of the leaves found at the end of the growth period (March 1998) was higher than the data obtained by Carignan *et al.* (1994) during the low water phase (green leaves = 1.05%). However, the major effect of the prolonged flood on the water condition and over the concentration of nutrients of the green leaves was detected too late, when the extended flood regimes conclude (August 1998). During this period the value registered at site B is closed to the maximum green leaves nitrogen concentration measured by Carignan *et al.* (1994) in N-treated enclosures (TN= 2.58%) placed in this Site.

In these lakes, most of the phosphorus entering the floodplain was originated from the high suspended load of the Paraguay River. Annual biological demand appears to be much smaller than the amount of PO_4-P potentially supplied by the river by occasional large flood events (Carignan & Vaithiyanathan, 1999). Thus, N limitation and low N:P ratios are common in these floodplain lakes during low water phase. The isolation condition was characterized by increases in standing dead leaves density and decreases in the modal leaf length of the mature plants. Furthermore, in this condition, plants have a major development of the root system and more root weight per area (Poi de Neiff & Carignan, 1997). At Site C the increase in biomass of green leaves were similar to those obtained by Carignan et al. (1994) in the San Nicolás lake in control enclosures during the low water phase, where the production and biomass of *E. crassipes* were limited by nutrients. The P content of the green leaves in the artificial pond was close to the critical phosphorus requirement (0.13%) reported by Gerloff (1970) for submersed aquatic plants.

Given that the floodplain lakes become totally unconfined only by short periods of time, prolonged low water condition are infrequent in the Paraná River. Nevertheless, the total isolation of the floodplain could be found if the hydrological regime was modified by hydraulic works projected in the study area. In this case, the floodplain of the Paraná River may be isolated from the high suspended load supplied by the Paraguay River, which will probably affect negatively the biomass and production of free-floating aquatic macrophyte species.

Acknowledgements

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