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Litter decomposition of emergent macrophytes in a floodplain marsh of the Lower Paraná River

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Abstract

The role of litter decomposition on organic matter accumulation and nutrient cycling was studied in a floodplain marsh of the Lower Paraná River by means of in situ litterbag experiments. The effect of waterborne nutrients on decomposition rates was studied through a laboratory litterbag experiment. Litter decomposition was rather slow, remaining 40–50% of the initial mass after 2 years incubation. Similar decomposition rates were observed in laboratory and field experiments. Water fertilization did not significantly affect decomposition rates. Since organic matter production is faster than decomposition a net accumulation takes place in the upper layers of the marsh soil. N and P litter concentration increased during the decomposition experiment. Floodplain marshes represent effective sinks of nutrients through litter accumulation.

Keywords: Decomposition; Organic matter; Nutrients; Floodplain marshes; Emergent macrophytes; Paraná River

1. Introduction

High organic matter production has been quoted as a typical characteristic of floodplain marshes, and has been associated with high nutrient inputs from the river (Junk et al., 1989). Floodplain marshes occupy about 80% of the Paraná River deltaic surface. High emergent macrophyte primary production has been reported in the Paraná River floodplain marshes, being higher at the riverside strip of vegetation than inside the marsh (Villar et al., 1996). Most organic matter produced along the growing season falls down during winter and gives rise to the organic superficial layer of the marsh soil. Simultaneously with the

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decomposition process, the contribution of sediments transported by the river also takes place in this superficial layer, resulting in an important accretion rate (Villar et al., 1999a).

Litter alternatively releases and uptakes nutrients as it decomposes (Jordan et al., 1989). As mineralization proceeds further, it may gradually release nutrients again. Depending on which process predominates organic matter decomposition may represent a source or a sink of nutrients. The present contribution is aimed to determine the decomposition dynamics of aerial plant materials, the changes in nitrogen and phosphorus content of the materials, and its effect on the nutrient storage and cycling in a representative floodplain marsh of the Lower Paraná River. It is assessed if decomposition differed between the dominant species or between sites, close to the river or inside the floodplain and whether the external supply of nutrients affects litter decomposition rates.

2. Description of sites studied

The work was carried out in a floodplain marsh, at Puerto Constanza, on the left side of the Paraná Guazú River, about 50 km upstream from the mouth (Fig. 1). A large amount of water is daily exchanged between the river and the marsh, its magnitude depending on water level, tidal amplitude and wind action. The marsh was covered by a dense stand of emergent macrophytes, dominated by *Cyperus giganteus* and *Schoenoplectus californicus* (C.A. Mayer) Sójak. Both are elongate and slender species (2–3 m high and 1–2 cm diameter),

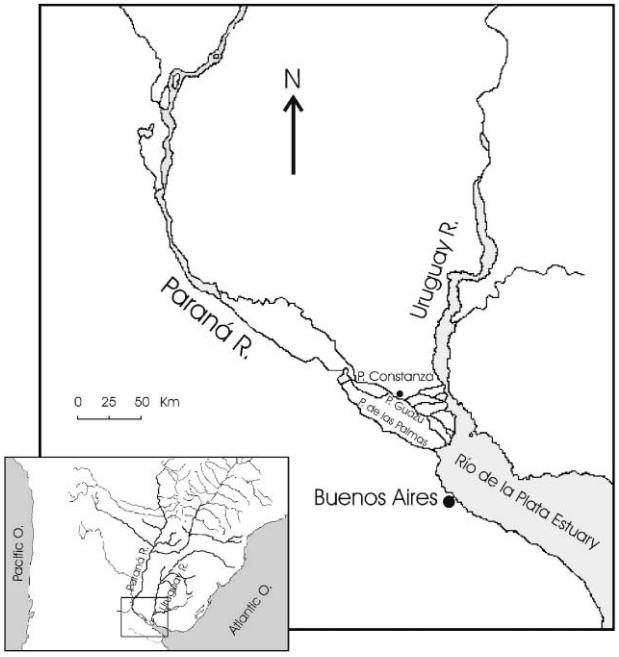

Fig. 1. Study site.

sustained by rhizomes. A small ridge at the river margin prevents the marsh from drying during low river water periods. Water depth in the marsh most often ranged 20–30 cm. The marsh surface was never dry, being the superficial litter layer always saturated with water.

3. Materials and methods

3.1. Litter decomposition

Two litterbag decomposition experiments were carried out in the field at two sites: about 50 m from the shoreline (riverside site) and about 600 m inside the marsh (inner floodplain site). Intact standing dry shoots of *S. californicus* were collected in the first experiment, and of *S. californicus* and *C. giganteus* in the second one. Shoots were cut into 10 cm length pieces and oven dried at 60°C. Litterbags were constructed from 15 cm × 20 cm rectangles of plastic net (2 mm openings). Each bag contained 43.5 and 20 g of dry shoots in the first and second experiment, respectively. Litterbags were placed in the water–sediment interface in the same site from which the plant material had been collected. They gradually became incorporated to the superficial sediment-litter layer of the marsh. The first experiment started on 8 September 1993 and three replicate bags were retrieved after 6, 20, 50, 190 and 230 days of incubation. The second experiment started in May 1994, and 5–6 replicate bags were retrieved after 8, 15 and 22 months of incubation. Litter remaining in the retrieved bags was carefully separated from roots growing inside them. The fragments of macrophytes were washed gently in distilled water and any attached seston and periphytic material was carefully scraped off. The material was dried at 60°C, weighed, ground and analyzed for P (Andersen, 1979), N and C (C–N analyzer) concentrations. Total N and P per bag was assessed by multiplying the mass weight in each bag by its N or P content.

In order to study the effect of waterborne N and P concentrations on litter decomposition rates, a litterbag experiment was performed at the laboratory. Litterbags containing *C. giganteus* dry shoots were constructed in the same way as for the field experiments and incubated in the dark, at room temperature, in plastic enclosures of 50 cm diameter and 80 cm height, filled with 91 of Paraná River water. One set of samples was incubated without any addition (control treatment), another set was enriched with $(NH_4)_2SO_4$ and the other with Na_3PO_4 to attain a concentration of 3 mg N l^{-1} and 0.7 mg P l^{-1}, respectively. The N and P additions were repeated on days 45, 120, 242, 307 and 444. The experiment started on 13 December 1993, and the bags were retrieved by triplicate after 17, 65, 412 and 781 days. Retrieved litterbags were treated in the same way as for the field experiment.

3.2. Water analysis

Water pH, dissolved oxygen, inorganic N and *o*-P concentrations were measured in coincidence with litterbags retrieval through the field and laboratory experiments. In the former, both marsh sites were simultaneously sampled. Dissolved oxygen was determined with a YSI 51B recorder and pH with an Orion 250A pH meter. Water samples were filtered through Whatman GF/C filters, and carried in ice to the laboratory. Dissolved nutrients were determined in the filtrate. *o*-P (molybdate-ascorbic acid) and NO_3^- plus

NO_2^- (cadmium reduction followed by diazotation) were determined following Strickland and Parsons (1972). NH_4^+ (indophenol blue) was measured according to Mackereth et al. (1978).

3.3. Statistical analysis

Limnological variates data, nutrient concentration in water and in litter material, and litter dry weight were tested for normality and homogeneity of variance using the Lilliefors and Bartlet tests, respectively (Sokal and Rohlf, 1980). Two way ANOVA were performed to compare litter dry weight and N and P concentration in the retrieved material at each sampling date, being plant specie and sampling site the main factors.

The dry weight remaining in the litterbags was plotted against time (in days) to examine the pattern of litter breakdown, and curves fitted to the data to test the most appropriate form of equations in order to describe the pattern. The equations were fitted by regression analysis and the significance was tested using covariance analysis. Two models were applied to describe the loss of mass over time.

1. A linear equation that assumes that decomposition rate is constant within time

$$W_t = W_o - kt$$

2. An exponential equation which assumes that a constant fraction k of the mass remaining decays in each time unit

$$W_t = W_o\, e^{-kt}$$

where W_o is the initial weight; W_t the weight at time "t"; k the decay constant; and t time in days.

Randomized block ANOVA (Sokal and Rohlf, 1980) were performed to compare water chemical data between both marsh sampling sites. Sites were considered the main factor and sampling dates the blocking factor. Software used was Statistica (1993).

Table 1
First litterbag decomposition experiment[a]

	Riverside		Inner floodplain	
	DW	P	DW	P
8 September 93	43.5		43.5	
14 September 93	41.1 ± 0.4	0.23 ± 0.07	41.7 ± 0.2	0.32 ± 0.03
28 September 93	42.2 ± 1.3	0.19 ± 0.03	41.9 ± 1.3	0.27 ± 0.05
26 October 93	42.5 ± 0.2	0.17 ± 0.03	42.0 ± 0.7	0.17 ± 0.02
21 February 94	40.6 ± 0.7	0.22 ± 0.02	41.5 ± 0.4	0.24 ± 0.04
30 March 94	36.0 ± 2.4	0.40 ± 0.02	37.0 ± 0.9	0.43 ± 0.09

[a] Dry weight (D.W., g) and P content ($\mu g\ g^{-1}$) of *S. californicus* shoot litterbags at the Puerto Constanza marsh (mean ± standard deviation, $n = 3$).

4. Results

The first field decomposition experiment concluded after 7 months attaining a dry weight loss of 15–17% (Table 1). Litter P concentration initially decreased through the first 48 days followed by a subsequent increase.

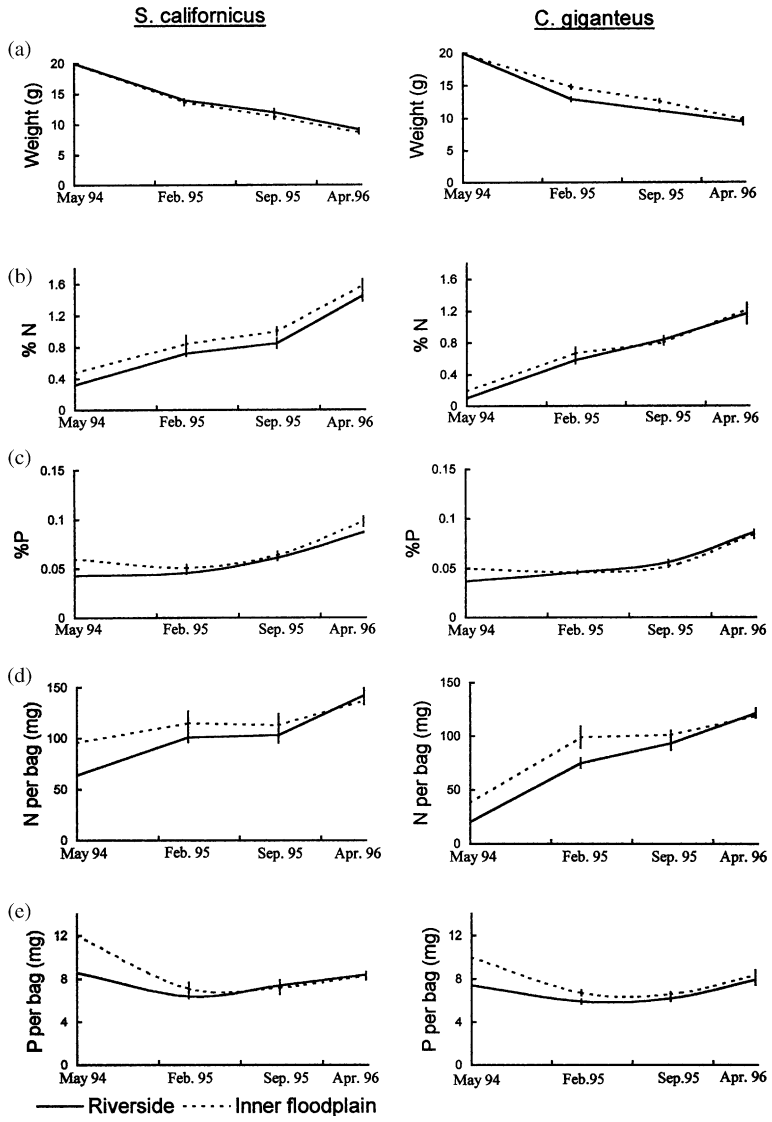

Fig. 2. Litter dry mass (a), tissue N concentration (b), tissue P concentration (c), total N content per bag (d) and total P content per bag (e) of *S. californicus* and *C. giganteus* shoots retrieved throughout a litterbag decomposition experiment held in the riverside and inner floodplain marsh of the Lower Paraná River (mean ± standard error, $n = 5$).

Table 2
Estimation of the degradation constants (k) and parameters of the significance tests of the laboratory and field decomposition experiments[a]

	k	Model F ratio	P	r^2
Laboratory experiment				
Control				
Linear	0.0153	23.8	0.016	0.89
Exponential	0.0013	61.4	0.004	0.95
Nitrogen				
Linear	0.0150	16.6	0.026	0.85
Exponential	0.0012	28.7	0.013	0.91
Phosphorus				
Linear	0.0175	142.2	0.015	0.89
Exponential	0.0016	73.0	0.003	0.96
Field experiment				
Riverside				
S. californicus				
Linear	0.0149	56.0	0.017	0.99
Exponential	0.0011	160.8	0.006	0.99
C. giganteus				
Linear	0.0147	19.4	0.048	0.91
Exponential	0.0011	42.7	0.023	0.96
Inner floodplain				
S. californicus				
Linear	0.0157	55.6	0.018	0.97
Exponential	0.0012	272.2	0.004	0.99
C. giganteus				
Linear	0.0143	113.6	0.008	0.98
Exponential	0.0010	247.3	0.004	0.99

[a] Fitted models are linear and exponential with time.

The second field decomposition experiment showed that almost half of the litter matter remained within the bags after 22 months (Fig. 2). *C. giganteus* showed faster mass loss in the riverside site through the first 8 months ($P < 0.01$), weight differences were maintained until 16 months ($P < 0.01$), and blurred at the end of the experiment. In the last sampling remaining litter mass was higher for *C. giganteus* ($P < 0.01$) which showed the lower tissue N content. The fit of the experimental data to the decomposition models is shown in Table 2. Both, exponential and linear models described similarly well the experimental data, showing high and significant correlation coefficients. No significant differences were found in the degradation constants between macrophyte species (*S. californicus* versus *C. giganteus*) neither between sampling sites (riverside versus inner floodplain).

Litter N concentration increased throughout the experiment (Fig. 2). N gains were larger where the initial N concentrations were lower: *C. giganteus* at the riverside increased its N concentration 12 times throughout the experiment while *S. californicus* at the same site showed a 4.5-fold increase. Initial differences in N concentration decreased throughout the experiment. The N content per bag increased along the experiment in both sites and species.

Table 3
Limnological variates measured at the floodplain marsh throughout the 11 samplings performed during the in situ litterbag decomposition experiments[a]

	Riverside marsh		Inner floodplain marsh	
	Mean	Range	Mean	Range
Temperature (°C)	17	7–23	15	7–18
Conductivity ($\mu S\,cm^{-1}$)	175	112–282	131	110–143
Oxygen ($mg\,l^{-1}$)	1.9	0.4–3	1.9	0.4–3
pH	6.3	5.5–6.8	6.0	5.7–6.3
o-P ($\mu g\,l^{-1}$)	122	23–300	70	15–167
N-($NO_3^- + NO_2^-$) ($\mu g\,l^{-1}$)	26	4–34	16	nd–108
N-NH_4^+ ($\mu g\,l^{-1}$)	44	9–181	38	4–46

[a] nd: not detectable.

During the first 8 months litter P concentration decreased where the initial P concentration was higher (*S. californicus* at the inner floodplain site; Fig. 2), remained unchanged at intermediate initial P concentration (*S. californicus* at the riverside and *C. giganteus* at the inner floodplain site), while increased where initial concentration was lower (*C. giganteus* at the riverside site). Later, P concentration increased in all treatments and did not show significant differences between sites. Unlike N, increased P concentration in the decomposing

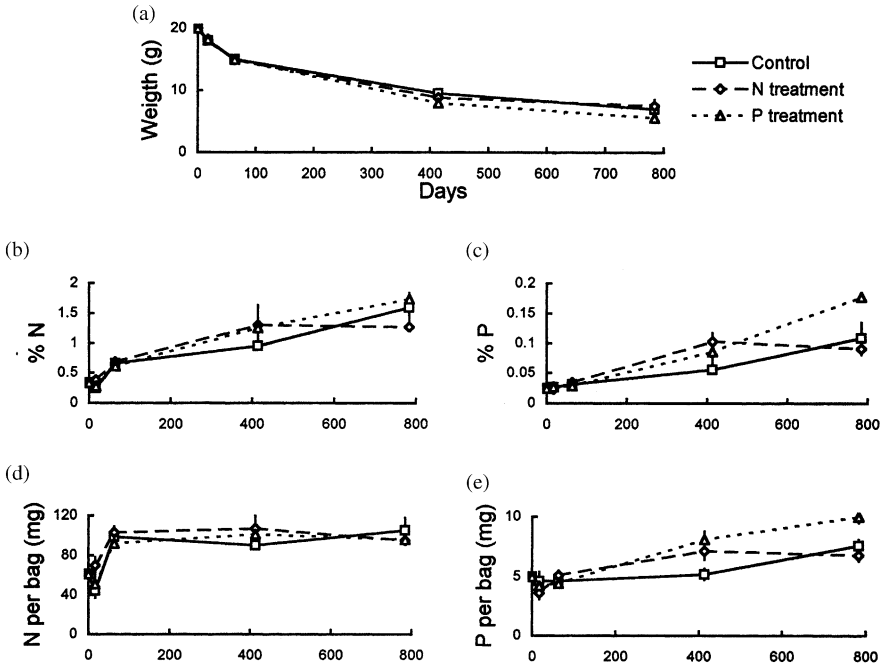

Fig. 3. Litter dry mass (a), litter N (b) and P (c) concentrations and N (d) and P (e) content per bag of *C. giganteus* shoots in a laboratory litterbag decomposition experiment (mean ± standard error, $n = 3$).

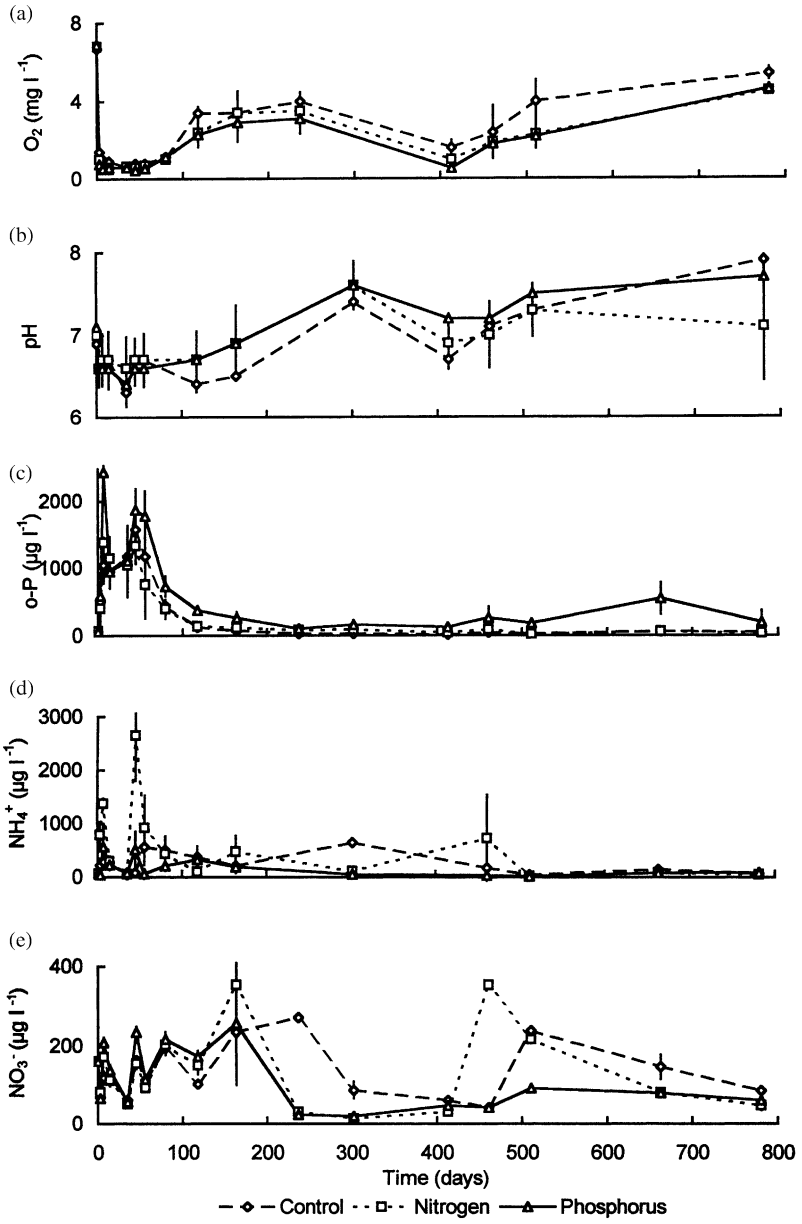

Fig. 4. Changes in dissolved oxygen (a), pH (b), *o*-P (c), NH_4^+ (d) and $NO_3^- + NO_2^-$ (e) concentration in a laboratory *C. giganteus* litterbag decomposition experiment (mean ± standard error, $n = 3$).

litter material of both species was counterbalanced by litter mass loss, leading to unchanged P content per bag at the riverside site and lower P content per bag at the inner floodplain site at the end of the experiment. N/P litter ratio (by weight) increased from 2.7–3.8 (*C. giganteus*), and 7.4–8.0 (*S. californicus*) at the beginning to 14.0–17.0 at the end of the experiment.

Oxygen, pH and inorganic N concentrations in water did not show significant differences between marsh sites (Table 3). Inorganic nitrogen to *o*-P ratio (by weight) in the floodplain was 0.6.

The laboratory experiment showed that decomposition rates in the N and P enriched treatments were not significantly different from the control (Fig. 3, Table 2). Decomposition rates were similar in the laboratory than in the field experiment. N concentration in the litter material decreased in the first sampling of the control and P enriched treatment to increase later throughout 28 months without attaining significant differences between treatments. After the initial decreased in the control, N content per bag also increased in all treatments at the beginning of the experiment. Later on, mass losses counterbalanced increased concentration within the litter material. P concentrations increased through the incubation period being higher in the P enriched treatment ($P < 0.05$). P content per bag slightly increased in the control and N enriched treatment being higher in the P enriched treatment.

Within the laboratory enclosures, dissolved oxygen was low (0.5–1 mg l^{-1}) for the first 3 months (Fig. 4), and showed some higher values (2–6 mg l^{-1}) throughout the rest of the incubation period, without significant differences between treatments. NH_4^+, *o*-P and to a less extent NO_3^- water concentrations were strongly increased through the firsts weeks, showing high variability, followed by a subsequent decrease of the formers which lasted until the end of the experiment. NO_3^- and NH_4^+ concentrations in the N enriched treatment were significantly higher than in the other treatments only for a few days after each N addition. The P enriched treatment showed higher *o*-P concentration in water along the experiment.

5. Discussion

Low decomposition rates of the dominant macrophytes determine that organic matter production proceed faster than decomposition. The combined effect of high macrophyte production (Villar et al., 1996) and low decomposition rates (this study) results in a net accumulation of detritus. The degradation constants estimated in the present paper for both species look rather low when compared with the literature (Godshalk and Wetzel, 1978a; Brinson et al., 1981; Rogers and Breen, 1982; Hammerly et al., 1989), pointing to a relatively slow litter decomposition in the Paraná deltaic marshes. Decomposition rates were lower than reported for 12 different plant species from the Middle Paraná stretch (Leguizamon et al., 1992) and similar to those of *Spartina maritima* in a salt marsh of Northern Spain (Pozo and Colino, 1992). Percent of weight remaining in litterbags after in situ incubation was higher than reported for *Spartina alterniflora* in a New England salt marsh, USA (Valiela et al., 1985) and similar to reported figures for *Typha angustifolia* in a brackish tidal marsh in Virginia, USA (Jordan et al., 1989) and for *Cladium jamaiquensis* and *Typha dominguensis*, in the Florida Everglades, USA (Davis, 1991). Decomposition rates were

not stimulated by N or P addition. Although it is often assumed that available nutrients influence decomposition rates, Jordan et al. (1989) and Howard-Williams et al. (1988) reported no effect of nutrient addition on decomposition rates, quoting several studies which reported similar results, and suggesting that nutrient supply is not always a limiting factor for decomposition and immobilization. Godshalk and Wetzel (1978b) reported that decay rates of different macrophytes were correlated with the total amount of fiber constituents present in the tissue, which, in turn, was correlated with the C/N ratio. Comparing decomposition rates of different macrophytes they reported that the emergent bulrushes showed the lowest decay rates associated with the highest C/N ratio. They also showed the strong influence of temperature and oxygen concentration in the decomposition rates. It seems likely that the community structure dominated by high C/N species and the low oxygen concentration prevailing year round determine the slow decomposition rates observed in the Paraná deltaic marshes.

Although most studies on decomposition rates are fitted to exponential models, good fit to linear models have also been reported (Rogers and Breen, 1982; Pozo and Colino, 1992). Our results are consistent with Brinson et al. (1981) observation that the difference between linear and exponential models is small after 1 year and negligible for slower rates of loss.

Decomposition initially released nutrients by leaching as could be inferred from the initial decrease in tissue P content in the first field experiment and the tissue N content in the control of laboratory experiment, consistent with the initial increases in dissolved nutrients in the water of enclosures. This phase was later followed by a longer one of litter enrichment, resulting in an increased litter N and P concentrations in the laboratory and second field experiments, consistent with the simultaneous decrease of the dissolved nutrient concentrations in the water of the laboratory enclosures. Decomposing material gradually enriched its N and P concentration throughout the experiment, but N in a larger proportion. Our findings were coincident with those of Davis (1991) and Jordan et al. (1989). A net gain or loss resulted from the combined effect of changes in tissue concentration plus loss of matter in each bag. Increased litter P concentration was counterbalanced by decreased mass content resulting in roughly no change of the total P content per bag. Alternate release and uptake from the litter compartment cannot explain the higher *o*-P concentrations previously reported in the marsh than in the river. Partial dissolution of riverine suspended matter upon settlement in the acid and oxygen depleted marsh environment seems likely to be the main cause of this pattern (Villar et al., 1998).

Due to the high C/N ratio of the litter, N demands of decomposers cause the initial release phase to be later followed by the subsequent immobilization of exogenous N. Unlike P, increased litter N concentration represents a higher demand that could be contributed by the mineralization within the bags, determining a net gain of N throughout the incubation period. Net increases in the nitrogen content of decomposing macrophyte tissue have been recorded and attributed to accumulation of microbial protein (Godashlk and Wetzel, 1978b). N concentration in the upper layers of the marsh sediments (Villar et al., 1999b) is higher than in the macrophytes standing dry shoots and than in the river suspended matter (Bornetto et al., 1994), suggesting that the Paraná River floodplain marshes retain large amounts of N by the combined effect of detritus production plus later nutrient enrichment. This trend is consistent with the lower inorganic N concentrations observed in the marsh compared with the river water (Villar et al., 1998). Oxygen and NO_3^- depletion in marsh enclosures filled

with river water was interpreted as result of denitrification in the water–sediment interface. Present evidence suggests that litter enrichment might also be an important N fate within the marsh.

6. Conclusion

The combined effect of high macrophyte production, litter fallout and low decomposition rates is the net accumulation of detritus.

The Paraná River floodplain marshes represent large sinks of nutrients mainly stored in the organic matrix of the soil profile.

N and P retention is accomplished by the combined effect of litter production and fallout followed by later litter enrichment. N enrichment cannot be accounted for the amount of N originated in the mineralization of the detritus, and must be supplemented by the exogenous dissolved inorganic fraction.

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References

Andersen, J., 1979. An ignition method for determination of total phosphorus in lake sediments. Water Res. 10, 329–331.

Bornetto, C., de Cabo, L., Gabellone, N., Vinocur, A., Donadelli, J., Unrein, F., 1994. Nutrient dynamics in the deltaic floodplain of the Lower Paraná River. Arch. Hydrobiol. 131 (3), 277–295.

Brinson, M., Lugo, A., Brown, S., 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Ann. Rev. Ecol. Syst. 12, 123–161.

Davis, S.M., 1991. Growth, decomposition and nutrient retention of *Cladium jamaiquense* Crantz. and *Typha dominguensis* Pers. in the Florida Everglades. Aquat. Bot. 40, 203–224.

Godshalk, G., Wetzel, R.G., 1978a. Decomposition of aquatic angiosperms. II. Particulates components. Aquat. Bot. 5, 301–327.

Godshalk, G., Wetzel R. G., 1978b. Decomposition in the littoral zone of lakes. In: Whigham, D.F., Simpson, R.L. (Eds.), Freshwater Wetlands: Ecological Processes and Management Potential. Academic Press, New York, pp. 131–143.

Hammerly, J., Leguizamon, M., Maine, M., Schiver, D., Pizzarro, M., 1989. Decomposition rate of plant material in the Paraná Medio River. Hydrobiologia 183, 179–184.

Howard-Williams, C., Pickmere, S., Davies, J., 1988. The effect of nutrients on aquatic plant decomposition rates. Verh. Int. Verein. Limnol. 12, 1973–1978.

Jordan, T.E., Whigham, D.F., Correll, D.L., 1989. The role of litter in nutrient cycling in a brackish tikal marsh. Ecology 70, 1906–1915.

Junk, W., Bailey, P., Sparks, R., 1989. The flood pulse concept in river-floodplain systems. Can. Spec. Publ. Fish. Aquat. Sci. 106, 110–127.

Leguizamon, M., Hammerly, J., Maine, M., Suñe, N., Pizzarro, M., 1992. Decomposition and nutrient liberation rates of plant material in Paraná medio River (Argentina). Hydrobiologia 230, 157–164.

Mackereth, F., Heron, J., Talling, J., 1978. Water analysis: some revised methods for limnologists. Freshwater Biol. Assoc. Scientific. Publ. No. 36.

Pozo, J., Colino, R., 1992. Decomposition processes of *Spartina maritima* in a salt marsh of the Basqu Country. Hydrobiologia 231, 165–175.

Rogers, K.H., Breen, C.M., 1982. Decomposition of *Potamogeton crispus* L.: the effects of drying on the pattern of mass and nutrient loss. Aquat. Bot. 12, 1–12.

Sokal, R., Rohlf, F., 1980. Biometría. Principios y métodos estadísticos en la investigación biológica. H. Blume Ediciones, Madrid.

Statistica, 1993. Statistica for windows. Release 4.3. Copyright Statsoft Inc.

Strickland, J., Parsons, T., 1972. A practical handbook for seawater analysis. Bull. 167. J. Fish. Res. Bd. Canada, Ottawa.

Valiela, I., Teal, J., Allen, S., Etten, R., Goehringer, D., Volkmann, S., 1985. Decomposition in slat marsh ecosystems: the phases and major factors affecting disappearance of above-ground organic mater. J. Exp. Mar. Biol. Ecol. 89, 29–54.

Villar, C., de Cabo, L., Bonetto, C., 1996. Macrophytic primary production and nutrient concentrations in a deltaic floodplain marsh of the Lower Paraná River. Hydrobiologia 330, 59–66.

Villar, C., de Cabo, L., Vaithiyanathan, P., Bonetto, C., 1998. River-floodplain interactions: nutrient concentrations in the Lower Paraná River. Arch. Hydrobiol. 142, 433–450.

Villar, C., Vaithiyanathan, P., Bonetto, C., 1999a. Impact of sea level rise on coastal marshes of the Lower Paraná River and the Río de la Plata Estuary. Curr. Topics Wetland Biogeochem. 3, 182–193.

Villar, C., de Cabo, L., Vaithiyanathan, P., Bonetto, C., 1999b. Porewater N and P concentration in a floodplain marsh of the Lower Paraná River. Hydrobiologia 392, 65–71.