LEAF LITTER DECOMPOSITION IN THREE WETLAND TYPES OF THE PARANÁ RIVER FLOODPLAIN

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Abstract: Leaf decomposition rates of nine types of litter, ranging in lignin content from 1.04 to 25.71%, were measured at three wetlands with different inundation regimes and related to internal and external factors. In these sites (located in the alluvial floodplain along at transect perpendicular to the main channel of the Paraná River), 180 litter bags were incubated under water. To test the importance of initial nitrogen, lignin, phosphorus, or L:N content of the litter in predicting decay rates, we analyzed the relationship between leaf quality and dry weight remaining (at 30 days and at the end of the incubation) within each wetland and under uniform environmental conditions. To elucidate the effects of environmental factors (especially hydroperiod) on decomposition processes, we compared the decay coefficient of one of these species (*Eichhornia crassipes*) across the three wetlands. Our results strongly suggest that under uniform environmental conditions, decomposition rates were best explained by a single internal factor related to litter quality. We found two different situations. 1) In the marsh with riverine forest, where decomposition was rapid and the half-life of the litter ranged from 9.6 to 63 days, the initial nitrogen content of leaves was a good predictor of decay rates both at 30 days and at the end of the incubation. 2) In the oxbow lake and palm swamp forest, where decomposition was lower and the half-life varied between 31.5 and 219 days, the L:N explains the variability on dry weight remaining at the end of the incubation. The decay coefficient of *E. crassipes* across sites was significantly related to NO_3^- concentration of water. We concluded that both environmental variables (i.e., the fluvial quotient of connectivity and the number of days in high water) and leaf litter quality (i.e., nitrogen content and L:N) are important factors regulating leaf litter decomposition in Paraná River floodplain wetlands.

Key Words: litter decomposition, Paraná River, riparian wetlands, hydroperiod

INTRODUCTION

Floodplain wetlands are among the most productive ecosystems and are often characterized as having large inputs of detritus. This suggests that the floodplain may serve as a temporary storage area for detritus such as leaf litter before its entry into the stream (Merritt and Lawson 1992).

In temperate regions, the majority of litter input occurs in the autumn, and decomposition begins almost immediately after litterfall (Odum et al. 1973). In contrast, in the Paraná River floodplain, the amount of litter produced varies depending on the species composition and the hydrologic regime of the river (Neiff and Poi de Neiff 1990). The maximum litterfall (daily average 2.83 $g.m^{-2}day^{-1}$) of *Copernicia alba* Morong.,

one of the most frequent palms of South American floodplains (Neiff 2001), was recorded when the palm swamp forest was flooded (Poi de Neiff and Casco 2001). In comparison, the highest leaf litterfall of *Tessaria integrifolia* Ruiz et Pav. (a dominant tree of the Paraná River pioneer forest) was recorded during a prolonged low water phase (2.91 $g.m^{-2}day^{-1}$, Neiff and Poi de Neiff 1990). However, during extreme floods, the riverine forest can remain submerged for more than three months, and the leaves may be completely lost by abscission.

Decomposition is a complex process that is regulated by physical, chemical, and biological processes. The rate of decomposition has been related to the chemical quality of the litter and to the environmental

conditions where the process occurs (Webster and Benfield 1986). Considerable evidence has demonstrated the importance of dissolved oxygen concentration, acidity, temperature, and dissolved nutrient concentration to leaf decomposition (Wetzel 1990, van der Valk et al. 1991, Pagioro and Thomaz 1999, Bianchini 2003). Several studies have found relationships between substrate quality indices, such as Carbon: Nitrogen or Lignin: Nitrogen, and rates of mass loss for leaf litter (Melillo et al. 1982, Taylor et al. 1989). Ostrofsky (1997) noted that decomposition rates were affected by a combination of nutritional refractoriness and deterrents (total phenolics) variables. Under climatically similar conditions, flooded sites have more rapid decay than adjacent upland sites (Brinson 1977, Merritt and Lawson 1979, Day 1982, Junk et al. 1989, Conner and Day 1991, van der Valk et al. 1991, Merritt and Lawson 1992, Furch and Junk 1997).

Water inputs are the major source of nutrients to riparian wetlands (Mitsch and Gosselink 1993). Hence, small changes in hydrology can modify chemical and physical properties such as nutrient availability, degree of anoxia, sediment properties, and pH. However, considering the scarcity of studies on such ecosystems and the great variability among wetland types, it is not surprising that relationships between frequency and duration of flooding and decomposition rates have not been found (Brinson et al. 1981, Mitsch and Gosselink 1993).

Floodplains of large rivers encompass an array of ecosystem types and flooding regimes (Junk et al. 1989, Neiff 1990). In the Low Paraná River, a seventh order stream, at least seven natural plant community types occur (Neiff 1986). The form and quality of macrophytic vegetation vary greatly among these different plant communities. Aquatic habitats produce principally herbaceous plant tissue in the form of floating and submerged macrophytes. Forest vegetation produces leaf litter with wide ranges in quality (Neiff and Poi de Neiff 1990, Poi de Neiff and Casco 2001).

Leaf decomposition rates of nine types of litter were measured in three wetlands with different inundation regimes and related to internal (initial nitrogen, lignin, phosphorus, or L:N content of the litter) and external factors (water temperature, dissolved oxygen, conductivity, pH, and nutrients concentration). In comparative field studies, both factors interact to determine decomposition rates, so this study was designed to minimize this problem. To test the importance of internal factors in predicting decay rates, we analyzed the relationship between leaf quality and dry weight remaining within each wetland and under uniform environmental conditions. To elucidate the effects of external factors (especially hydroperiod) on decomposition processes, we compared the decay coefficient of one of these species

(the free floating macrophyte *Eichhornia crassipes* (Mart.) Solms) across three sites with different physical, chemical, and hydrologic conditions.

Our hypothesis was that leaf litter in the site with high flooding frequency decomposes rapidly and decay rates would have a strong correlation with initial nitrogen content of the litter. In contrast, sites that are briefly inundated would have slow decomposition and other litter quality factors would be better predictors of decay rates.

METHODS

Study Sites

The study area is on the west bank of the Paraná River, 30 km downstream from the confluence with the Paraguay River. On this margin, the alluvial floodplain is 8 km wide, with several types of wetlands (Neiff 2001). The east bank is flanked by an 8- to 10-m high terrace.

The hydrologic regime of the Paraná River is irregular, with normal floods 1–3 times per year and extreme floods attributed to ENSO (El Niño Southern Oscillation) events (Núñez and Vargas 1998). At Corrientes (Argentina), the mean discharge is 16.000 m^3s^{-1}, with a maximum of 60.000 m^3s^{-1} corresponding to flow velocities 0.4–2.0 m s^{-1} during regular floods (Neiff et al. 2000).

The study area has hot summers and mild winters. Mean monthly maximum temperature based on records of a nearby weather station was 32° C (January), and the minimum was 9.2° C (July). The annual rainfall was 1598 mm.

The three sites used for the decomposition experiment were in the alluvial floodplain along a transect perpendicular to the main channel (Figure 1). Each site has a different inundation regime according to location along the geomorphological gradient. Marsh with riverine forest (Site A) located in sand bars near the main channel was connected with the Paraná River when the water level at nearby Puerto Corrientes was > 46.19 m.a.s.l., whereas oxbow lake with mixed gallery forest (Site B) and palm swamp forest (Site C) were flooded with stages of 47.24 m.a.s.l. and 47.69 m.a.s.l., respectively. A pulse has a high water phase when the river water enters the floodplain wetland and a low water phase when the wetland is isolated from the river.

Near the river, the marsh (27°28′09″S; 58°52′39″W, Site A) was colonized by floating (*Eichhornia crassipes*, -waterhyacinth) and rooted macrophytes (*Polygonum acuminatum* Kenth. smartweed and *Panicum elephantipes* Nees ex Trin -switchgrass). At sand bars, riverine forest typically has monospecific stands of
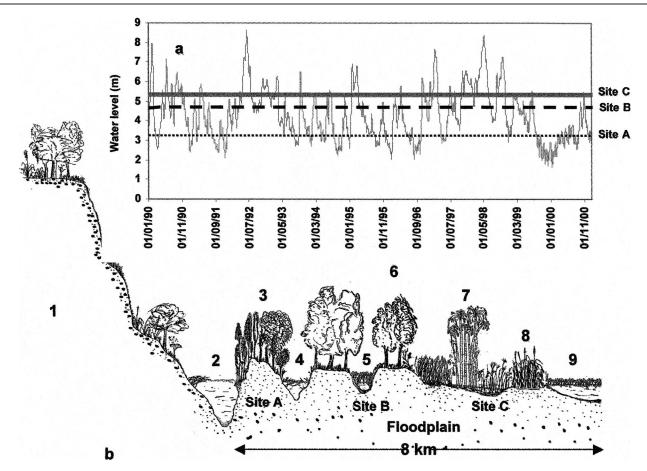
Figure 1.   a. Water-level fluctuations of Paraná River at Puerto Corrientes between 1990 and 2000. The sites were connected with the Paraná above the level indicated by the horizontal lines. b. Cross-section of floodplain Paraná River and its natural plant communities. References: 1: Left bank; 2: Paraná River; 3: Riverine forest (*Salix humboldtiana* and *Tessaria integrifolia*); 4: *Eichhornia crassipes*, *Polygonum acuminatum* and *Panicum elephantipes*; 5: Floating meadows (*Eichhornia crassipes*); 6: Mixed Gallery Forest (*Nectandra angustifolia*, *Peltophorum dubium*, *Banara arguta*); 7: Palm Forest (*Copernicia alba*); 8: Cattail (*Typha latifolia*); 9: Floating meadows *Eichhornia crassipes* and *Paspalum repens*.

rather uniform height (13 m) dominated by *Tessaria integrifolia* -alder or *Salix humboldtiana* Willd. -willow.

Site B is an oxbow lake (27°27′S; 58°51′W), 2 km away from the river. It is linear -to- crescent shaped (area=4.6 ha), shallow (mean depth= 1.55 m), and turbid (Secchi depths of 0.2 to 1 m). This lake sustains a large biomass of the floating macrophyte *E. crassipes*. Levees support mixed gallery forest dominated by the trees *Nectandra angustifolia* (Schrad.) Nees et Mart. -laurel, *Peltophorum dubium* (Spreng) Tanb. ibirá-pitá, and *Banara arguta* Briq. -granadillo.

The palm swamp forest (Site C; 27°26′S; 58°54′W) is 5 km from the Paraná River. *Copernicia alba* (palm) grows in pure stands about 13 m tall, with a mean diameter at breast height (dbh) of 22 cm. Stands of herbaceous aquatic plants, which did not grow on the forest floor but in the depressions of the swamp, are dominated by *Typha latifolia* L. -wide leaved cattail

and a mixture of *Paspalum repens* Bergius -water paspalum and *E. crassipes*.

Experimental Design and Analyses

Leaf decomposition was measured by the litter bag method (Crossley and Hoglund 1962). We used nine types of leaf litter from different species of trees and macrophytes, each dominant in one of the three sites described above. *Eichhornia crassipes* grows in all sites. The species were chosen on the basis of expected differences in nutrient (N and P) and lignin content. Forest leaves were collected by using litter traps placed at each site during August 1998. *Tessaria integrifolia* and *Salix humboldtiana* leaves were collected from younger stands 0.50–1 m high. We collected standing dead and wilted leaves of macrophytes at the end of the annual growing season (July).

During September 1996, 15 litter bags of 5 species

(*T. integrifolia*, *S. humboldtiana*, *P. acuminatum*, *P. elephantipes*, and *E. crassipes*) were placed in the marsh (Site A, n= 75). At the oxbow lake, we incubated 15 litter bags filled with *E. crassipes* leaves under floating meadow that cover up 70% of the water surface. For the mixed gallery forest, two groups of bags were prepared: 15 litter bags were placed under floating meadows, and 15 litter bags were placed in open water to determine differences in mass losses between these situations (Site B, n= 45). In the palm swamp forest (Site C, n= 60), 15 litter bags of each species (*P. repens*, *E. crassipes*, *T. latifolia*, and *C. alba*) were submerged in September 1998.

Nylon litter bags of 20 × 30 cm (palm) or 20 × 20 cm (all others) of 2- mm mesh were filled with 20 or 10 g of leaves, respectively. Air-dried leaves were used because pre-drying plant material at 105°C affects weight loss and nutrient release (Gopal et al. 1982).

According to previous published information (Neiff and Poi de Neiff 1990, Bruquetas de Zozaya and Neiff 1991, Poi de Neiff and Casco 2001), leaf litter from *E. crassipes* and *T. integrifolia* decomposed rapidly near the river while leaves from palm decayed slowly at sites located farther from the river. Because almost 50% of the litter must decompose during the incubation, triplicate samples were collected at different time intervals in each of the study sites: 7, 17, 24, 30, and 40 days (riverine forest); 7, 17, 30, 68, 97 (oxbow lake) or 7, 30, 40, 68, 97, or 125 days (swamp palm forest).

One set of leaf bags was removed, and each bag was packed separately in plastic bags in the field and was returned to the laboratory. Leaf material was gently washed on a sieve (125-μm mesh) to remove silt, epiphytes, and invertebrates.

The remaining plant material was dried to a constant weight at 105°C. When mass losses were calculated, corrections were made for moisture content of air-dried samples up to constant dry weight (105°C).

The decomposition constant k (Olson 1963) for the exponential model was calculated using the equation:

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

where W_0 is the original amount of litter; W_t is the amount of litter remaining after the time t, and t is the time in days.

We applied the negative exponential model based on dry weight remaining because it is widely used in temperate (Webster and Benfield 1986, Magee 1993) and tropical ecosystems (Gopal et al. 1982, Hammerly et al. 1989, Pagioro and Thomaz 1999, Bianchini 2003) to describe decomposition rates.

Physical and chemical data were taken at each site at the end of each incubation. Electrical conductivity, dissolved oxygen, and pH were recorded using a Checkmate 90 (Corning) conductimeter, a Oxi- 330 portable oximeter (WTW), and digital pH meter-330 (WTW), respectively. Water samples were filtered within 1–2 h of collection on pre-washed Gelman DM-450 (0.45 μm-pore) membranes for spectrophotometric analyses of NH_4^+ (indophenol blue method), $NO_3^- + NO_2^-$ (called NO_3^-) by Cd reduction and total phosphorus (molybdenum blue method) with persulfate oxidation (APHA l995). At the same time, leaves from each site 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. The Fluvial Connectivity Quotient (Neiff and Poi de Neiff 2003) was calculated for the period 1996–1999 as follows:

$$FCQ = \frac{\text{number of flooded days}}{\text{number of isolated days}}$$

Statistical Analyses

The dissolved oxygen, temperature, conductivity, pH, and nutrient concentrations were tested, and where necessary, data were log-transformed. Single-factor analysis of variance with post hoc Tukey tests was used to test for significant differences between sites.

At each site, the influence of litter quality on the rates of decomposition was analyzed by forward stepwise multiple regression. We used the percentage of mass remaining for each species as the dependent variable and %N, %P, % lignin, and L:N as independent variables. These analyses were made after 30 days and at the end of the incubations. The logarithmic or arcsine square root procedure was used to normalize the distributions.

To test the relationship between environmental factors and decomposition rates, we used forward stepwise multiple regression between the decay coefficient of *E. crassipes* (k as dependent variable) across sites and dissolved oxygen content, pH, NO_3^-, NH_4^+, total phosphorus, and water temperature of each sites during the incubation time.

RESULTS

Abiotic Differences

The duration of low and high water phases and the number of pulses between 1990 and 2000 ranged widely based on an 11-yr record of National Division of Ports (Figure 1). Between January 1996 and January 1999, riverine forest was connected with the main channel during 818 days (77% of the time), whereas oxbow lake and palm swamp forest were flooded 528 (50%) and 423 days (40%), respectively (Table 1). In

Table 1. Mean values and standard error (S.E.) of physical and chemical variables of the three sites during the *in situ* decomposition experiments. In the last third columns are the results from ANOVA (F, d.f. and P value). Different letters indicate means statistically different (Tukey's test, p < 0.05). Hydrologic conditions and fluvial connectivity quotient (FCQ) of the three sites are in the last four rows.

| | Riverine Forest | | Oxbow Lake | | Palm Swamp Forest | | ANOVA | | |
	Mean	S.E.	Mean	S.E.	Mean	S.E.	F	d.f.	p Value
Water temperature (°C)	25.3[a]	0.01	24.5[a]	0.02	22.7[a]	0.02	2.17	2, 13	0.1506
Dissolved Oxygen ($mg \cdot l^{-1}$)	6.2[b]	0.05	1.3[a]	0.15	1.6[a]	0.05	20.18	2, 13	0.0001
Conductivity ($\mu S \cdot cm^{-1}$)	164[b]	0.03	202[b]	0.04	72.6[a]	0.03	46.69	2, 13	0.0001
pH	7.1[b]	0.002	6.5[b]	0.01	5.9[a]	0.01	16.74	2, 13	0.0004
$N-(NO_3^- + NO_2^-)$ ($\mu g \cdot l^{-1}$)	106[c]	0.02	2.9[b]	0.11	1.5[a]	0.48	23.77	2, 13	0.0001
$N-NH_4^+$ ($\mu g \cdot l^{-1}$)	54[b]	0.08	5.0[a]	0.20	24.5[a]	0.23	11.05	2, 11	0.0023
$P-PO_4^-$ ($\mu g \cdot l^{-1}$)	28[a]	0.08	49[a]	0.17	86.0[a]	1.81	0.30	2, 11	0.7462
Hydrologic Conditions Between January 1996–January 1999									
	Riverine Forest		Oxbow Lake			Palm Swamp Forest			
Number of days in high water	818		528			423			
Number of days in low water	248		519			622			
Number of pulses	7		13			11			
FCQ	3.29		1.02			0.68			

this period, the FCQ followed the sequence: Site A > Site B > Site C.

Water temperatures varied between 20 and 26.8°C (Table 1); however, no significant differences were found among the three sites (Table 1). The water was more acidic at the palm swamp forest and contained more dissolved oxygen at the riverine forest than at the other two sites. During the incubation, NO_3^- concentration was significantly different between sites and decreased with the distance from the river (Table 1). Although mean phosphorus concentration was highest in the palm swamp forest, there was no significant difference between sites.

Wide variation in the initial concentration of lignin, nitrogen, and phosphorus was noted among samples of each of the nine types of litter. *Copernicia alba* and mixed gallery forest had lignin content > 20%, whereas leaves of *T. integrifolia* and *E. crassipes* had high concentrations of nitrogen (> 2%, Table 2). Leaf litter composition of *Eichhornia crassipes* differed among sites. The leaves showed higher nitrogen and lower lignin content at Site A, where the nutrient water content was high, than at Sites B and C (Table 2).

Decomposition Rates in Relation to Litter Quality

Decomposition of leaf litter in the marsh with riverine forest was rapid (Figure 2, Table 2), and the half-life of the species ranged from 9.6 to 63 days. After 30 days, 14% dry weight was still remaining in *T. integrifolia*, and 30% was left in *E. crassipes* leaves. When we regressed dry weight remaining of five species (*P. acuminatum*, *E. crassipes*, *T. integrifolia*, *P.*

elephantipes, and *S. humboldtiana*) and litter quality variables, mass losses were significantly related to the initial nitrogen content of the leaves (Table 3). Stepwise multiple regression results in a model that explained 86.11% of the variation in the dry weight remaining at the end of the incubation. After 30 days, three variables were included in the model for predicting dry weight remaining (Table 3), but nitrogen content was the most important predictor.

At oxbow lake with mixed gallery forest, *E. crassipes* leaves showed greater losses than mixed gallery forest leaves both incubated under floating meadows (Figure 3). The decay coefficient of mixed gallery forest litter, obtained in open water of the oxbow lake and under floating meadow, was similar (Table 2). The estimated times for 50% decomposition of leaf litter varied between 31.5 and 110 days. At 30 days, all simple regressions between mass remaining and the litter quality variables were not significant (p>0.01), and multiple regression indicated that L:N explains only 21.9% of the variability. At the end of the experiment (97 days), L:N was the best predictor of mass losses, which explained 94.7% of the variability (Table 3).

At palm swamp forest, the dry weight remaining after 30 days varied between 72.6% and 88.0% (Figure 4). The rank in loss rates was *E. crassipes* > *P. repens* > *T. latifolia* > *C. alba* (Table 2), and the estimated times for 50% decomposition ranged between 34.6 and 219 days. After 125 days of incubation, only 28% weight loss of *C. alba* had occurred. At this site, L:N explained the variability in dry weight remaining (for-

Table 2.   Decomposition rates and composition of nine types of litter in the studied sites. L: Lignin; N: Nitrogen; P: Phosphorus. [1] Open water; [2] Under floating meadows.; k: decay coefficient; $t_{0.50}$ = half-life of the litter; R^2 indicated exponential curve fitting.

	Litter Composition				Decomposition		
	L%	N%	P%	L:N	k day^{-1}	$t_{0.50}$	R^2
Riverine forest							
Tessaria integrifolia	11.65	2.13	0.31	5.47	0.072	9.6	0.94
Salix humboldtiana	13.76	1.81	0.19	7.60	0.019	36.4	0.89
Polygonum acuminatum	3.9	1.60	0.25	2.44	0.022	31.5	0.95
Panicum elephantipes	5.60	1.47	0.21	3.81	0.01	63.0	0.96
Eichhornia crassipes	1.04	2.13	0.35	0.48	0.067	10.3	0.83
Oxbow lake							
Mixed gallery forest[1]	21.72	1.71	0.15	12.70	0.007	96	0.96
Eichhornia crassipes[2]	2.35	2.05	0.25	1.15	0.022	31.5	0.91
Mixed gallery forest[2]	21.72	1.71	0.15	12.70	0.006	110	0.973
Palm swamp forest							
Typha latifolia	18.2	1.28	0.035	14.22	0.004	169	0.987
Paspalum repens	3.38	1.39	0.22	2.43	0.008	85	0.95
Eichhornia crassipes	2.35	2.05	0.25	1.15	0.020	34.6	0.913
Copernicia alba	25.71	1.21	0.07	21.25	0.003	219	0.97

ward stepwise multiple regression, Table 3) at 30 days and at the end of the incubation.

When we regressed the dry weight remaining of all litter substrates in the three sites with four internal variables (Table 3), these factors were capable of explaining less than 53.5% of the variation in decomposition rates (Table 3). There were a group of factors related to external condition that was equally or more important.

Decomposition Rates in Relation to Environmental Factors

When we compared the decay coefficient (k) of the same substrate (*E. crassipes*) across sites that had dif-
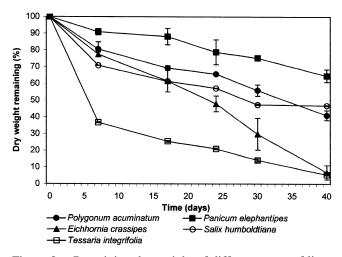

Figure 2.   Remaining dry weight of different types of litter at Site A (Marsh with riverine forest). The errors bars represent ± 1 SD.

ferent external variables (thus hydroperiod), decomposition was faster at Site A than at Sites B and C. Forward stepwise multiple regression indicated that NO_3^- concentration explains 93.1% of the variability in decomposition rates:

$$k = -0.00115259NO_3^- + 0.00416289\text{Temperature}$$

$$r^2 = 0.95 \qquad p < 0.05$$

These results support the hypothesis that the decomposition rates of the same litter substrate in the Paraná River wetland were positively affected by water NO_3^- content.

DISCUSSION

In the Paraná River floodplain, decomposition rates were in the range found in other ecosystems of the world (0.072 and 0.003 days^{-1}). For example, Nelson et al. (1990) reported k values between 0.0035 and 0.0019 days^{-1} for *Typha latifolia* in different freshwater marshes. The estimated half-life for *T. latifolia* litter incubated under and above a floating island (231 and 173 days^{-1}, respectively) and suspended in air (693 day^{-1}) in a cattail swamp (Bruquetas de Zozaya and Neiff 1991) were greater than the value of the present study (169 day^{-1}). At sites with alternating periods of standing water and exposure to air, leaf litter of *Copernicia alba* decomposed faster (Poi de Neiff and Casco 2001) than found here. Palm leaves in another palm floodplain forest also had low decomposition rates (Frangi and Lugo 1985).

Our decomposition rate for *Paspalum repens* was

Table 3. Results of a multiple linear regression analysis to test the relationship between dry weight remaining (at 30 days and at the end of incubation) and leaf litter decomposition. S.E.: standard error; Adj.: adjusted R^2; **significant at the $p < 0.01$; *not significant.

Dry Weight Remaining (30 days)				Dry Weight Remaining (end of the incubation)			
Parameter	Estimate	S.E.	Adj. R^2 (%)	Parameter	Estimate	S.E.	Adj. R^2 (%)
RIVERINE FOREST alone							
Constant	179.239	21.11	0.00	Constant	262.889	25.585	0.00
% Nitrogen	−20.609	2.246	82.67**	% Nitrogen	−29.609	3.285	86.11**
Litter Substrate	4.894	1.387	87.90**				
L:N ratio	1.767	0.790	90.93**				
OWBOW LAKE alone							
Constant	45.062	3.713	0.003	Constant	17.058	2.248	0.002
L:N ratio	0.693	0.412	21.99*	L:N ratio	2.387	0.249	94.78**
PALM SWAMP FOREST alone							
Constant	56.724	1.201	0.00	Constant	28.828	1.81	0.00
L:N ratio	0.5772	0.093	77.15**	L:N ratio	1.627	0.082	94.73**
				Lignin	−0.276	0.079	97.66**
AT 3 SITES							
Constant	104.42	22.114	0.00	Constant	24.392	3.41	0.00
% Nitrogen	−8.871	2.573	53.58**	L:N ratio	1.261	0.331	31.05**
Litter Substrate	2.522	0.808	63.78**				

lower than reported for *P. repens* from the main channel of the Paraná River (flow velocity = 0.6 m.s⁻¹) and the Colorado River (flow velocity = 0.03 m.s⁻¹) at Santa Fe, 600 km downstream (Hammerly et al. 1989). In contrast, the half-life for *E. crassipes* and *T. integrifolia* in the riverine wetland was shorter than other values obtained in the Paraná River (Poi de Neiff and Neiff 1989, Neiff and Poi de Neiff 1990).

Our results strongly suggest that, under uniform environmental conditions (within each wetland), decomposition rates were best explained by a single internal factor related to litter quality, as indicated by a mul-
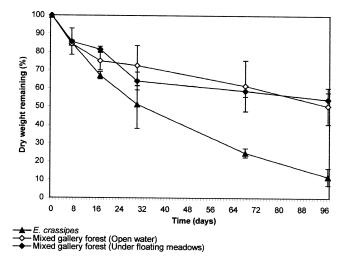
tiple regression using %N, %lignin, and L:N as independent variables. We found two different situations. 1) In the riverine wetland where decomposition is fastest, the initial nitrogen content of leaves is a good predictor of decay rates. 2) In the palm swamp forest and oxbow lake where decomposition is low, L:N ratio explains the variability of dry weight remaining at the end of the incubation. In the oxbow lake, the non-significant relationship between mass losses and L:N after 30 days, indicates that decomposition rates would be regulated by other internal factors. Taylor et al. (1989) showed that, for a wide range of litter lignin content, leaf mass remaining after two and after four
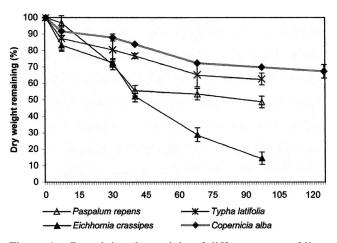

Figure 3. Remaining dry weight of different types of litter at Site B (Oxbow lake with mixed gallery forest). The errors bars represent ± 1 SD.

Figure 4. Remaining dry weight of different types of litter at Site C (Palm swamp forest). The errors bars represent ± 1 SD.

months was highly correlated with the C:N ratio. Ostrofsky (1997) found that a combination of internal factors (total phenolics, N content, and lignin) explained almost 50% of the variability of processing rates.

When nine types of litter with a wide range of lignin and nitrogen content were considered together (without considering the site which they grew), major independent variables were initial nitrogen concentration at 30 days and L:N at the end of the incubation. These results support findings that initial nitrogen composition of leaves influence decomposition rates during the first phase of litter decay, succeeded thereafter by lignin control (Berg 1986).

During the study period, the riverine forest was more connected with the river, received greater nutrient loads, and the *E. crassipes* leaf litter had higher nutrient concentrations than oxbow lake and palm swamp forest. Thus, decomposition of *E. crassipes* was faster at Site A than at Sites B and C. Our results are consistent with Brinson's (1993) observation that the position of wetlands in the drainage network, source of water, and chemical condition of inflow are important in decomposition process. Many studies using a variety of leaf types demonstrated faster breakdown in nutrient-rich systems than in nutrient-poor sites (Webster and Benfield 1986).

When we compared the decay coefficient of *E. crassipes* across sites, the multiple regression indicated that NO_3^- content of water is the more important external variable. Carignan and Neiff (1992) indicated that NO_3^- appearing in the Paraná River floodplain during the floods had a riverine origin, and NH_4^+ could not have been imported from the river since its concentration never exceeded 0.4 μmol.l^{-1} in the main channel before and during the floods. Compared to dissolved inorganic nitrogen, the phosphorus concentrations remain relatively high and change little during and after the flood. The decrease in NO_3^- concentration in riverwater as it flows through the Sites B and C may be due to uptake by aquatic plants and microorganisms, denitrification, and reduction to NH_4^+. This decrease is related to low pH and anaerobic conditions, but these variables were not selected by the multiple regression analysis. Nitrate concentration was also used as an indicator of hydrologic connectivity (between the nutrient-rich main channel and individual floodplain waters) in the Danube River (Tockner et al. 2000).

There was a clear relationship between hydroperiod and decomposition rates of *E. crassipes*. Because of the complexity of this study, we were unable to demonstrate environmental effects on decomposition when all species at the three sites were considered. However, the strong dependence of nitrogen litter concentration on decay rate at riverine forest and the importance of

L:N at oxbow lake and palm swamp forest indicate some indirect relationship with hydroperiod. We conclude that both environmental variables (i.e., the fluvial quotient of connectivity and the number of days in high water) and leaf litter quality (i.e., nitrogen content and L:N) are important factors regulating leaf litter decomposition in Paraná River floodplain wetlands.

The fate of organic matter will depend on three variables: (1) litterfall production, 2) the rate of decomposition, and (3) the hydrologic connection of the site with the larger fluvial system. At sites with greater production of litter and slowly decomposing material, there is more accumulation of detritus (i.e., *Copernicia alba*, at Site C) than sites with strong hydrologic connections and faster decomposition rates (i.e., *Tessaria integrifolia*, at Site A). The rapid decomposition and the slight tendency toward accumulation of soil organic matter is a characteristic of the riverine forests (Brinson 1990).

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