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Litterfall, leaf decomposition and litter colonization of *Tessaria integrifolia* (compositae) in the Parana river floodplain

Juan José Neiff & Alicia Poi de Neiff
Centro de Ecología Aplicada del Litoral, C.C. 291 (3400) Corrientes, Argentina

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Abstract

Litterfall and leaf decomposition rates were measured in Choui Island, 45 km downstream from the confluence of the Paraná and Paraguay rivers. The material was collected biweekly from April 1985 through September 1986. Decomposition was measured *in situ* by the litter bag technique.

Annual litterfall of *Tessaria integrifolia* gallery forest measured in the period April 1985 to March 1986 was 8.15 t ha^{-1}. Leaf litterfall was seasonal, i.e. significantly less leaf litter was shed during the high water phase than during the low water phase. The 'half life' of the *T. integrifolia* litter over 38 days of decomposition was 20 days. At the beginning of the experiment, 15 and 38 days subsamples of remaining detritus were analyzed in order to determine changes in the nutrient content. After 38 days of incubation, the order of nutrient disappearance was Ca > K > N > Mg > Na > P.

The number of invertebrates per g remaining litter of *Tessaria integrifolia* increased between incubations days 7 and 31. Collector-gatherers were more abundant after 38 days incubation; there were no shredders colonizing the leaf litter bags.

Introduction

Tessaria integrifolia forms extensive pure stands of pioneer gallery forest occupying up to 30000 ha along the Paraná and Paraguay rivers (Reboratti & Neiff, 1987) where the timing, frequency, intensity and duration of flooding are important. In mature populations, the litterfall produces an important input of organic matter which is incorporated into the fluvial systems.

Studies on litterfall production have been published for the inundation forest of Central Amazonas (Addis *et al.*, 1979; Franken *et al.*, 1979) and in the wetlands of North Carolina (Brinson, 1977; Brinson *et al.*, 1980), similar information for the Paraná gallery forests is still unavailable. Very little is known about decomposition and litter colonization of South American inundation forests (Irmler & Junk, 1982).

The objectives of the present study were: to estimate the litterfall of *Tessaria integrifolia* during the low- and high-water phase and to calculate the litter decay coefficient. A second objective was to categorize the invertebrates colonizing the *Tessaria integrifolia* litter according to feeding modes.

Study area

The Paraná System can be divided into two segments (Neiff, 1986). The High Paraná begins at the Paraná-Paraguay confluence and extends to the head-waters. This segment has a very variable width : depth radio, and a significant content of clay-loam detritus in the suspended load. The Low Paraná (below the Paraguay-Paraná confluence) flows southward as a typical floodplain river with an alluvial valley of 10 km width at Corrientes city; the talweg depth is 8–10 m; the mean discharge: 16000 $m^3 s^{-1}$, with a maximum value of 60000 $m^3 s^{-1}$ in extraordinary floods corresponding to flow velocities in the range 0.4–2.0 $m s^{-1}$ (Neiff, 1986).

After the Paraguay-Bermejo input, the suspended load is substantially increased (40–320 mg l^{-1}) with dominance of loam and fine sands in suspended and bottom sediments.

The study area is located on the sand banks of Choui Island on the right side of Paraná river (27° 30′ S, 58° 55′ W). There, *Tessaria integrifolia* forms typical monospecific stands of a rather uniform height (13 m) with younger stands 2 to 8 m high. The crown circumference is generally smaller than 2 m, the stem diameters at breast height lie between 3 and 20 cm and all the trees are monostemmed. The average density reaches 8000 trees ha^{-1} in unripe stands and declines to 7000 in mature populations. In this forest productivity can reach 37 t ha^{-1} yr^{-1}.

The initial contents of fiber components (as% of dry weight) of *T. integrifolia* leaves are hemicellulose: 9.5, cellulose: 19.2, lignin: 11.

The study site has hot summers and mild winters. The mean annual maximum temperature in the period September 1985-August 1986 was 28 °C and the minimum one 16.5 °C. Annual rainfall was 1598 mm. Water levels in the Paraná river during the study period are shown in the Fig. 1. Choui Island was flooded during April, May and mid-June 1985 and during May, June, July 1986.

During the incubation time the surface water temperature varied between 26 °C and 27.5 °C, the electrical conductivity between 133 $\mu S cm^{-1}$ and 235 $\mu S cm^{-1}$ and the pH between 7.0 and 7.3. The dissolved oxygen concentration ranged between 5 mg l^{-1} and 8.3 mg l^{-1}.

Secchi disk depth was 30 cm except after 38 days incubation when the value was 4 cm.

The mean nitrate concentration was 0.012 mg l^{-1} NO_3-N and the mean phosphate concentration was 0.02 mg l^{-1} PO_4-P.

Material and methods

Litterfall was collected biweekly during the 2-yr period from May 1985 through September 1986. Twenty-eight litter traps of 0.30 m^2 were distributed at random within a study area of 1 ha. The dry weights of leaf litter were compared statistically with ANOVA and tested at $P < 0.05$ (Steel & Torrie, 1980).

Leaf decomposition was measured in nylon net bags (20 × 20 cm) with a mesh size 2 mm. Samples of air dried leaves (10 g) were incubated under water in a secondary branch of Paraná river which enters in Choui Island. The *in situ* experiment (started on October, 1986) were performed in triplicate at 7, 15, 24, 31 and 38 days. At the end of each incubation time, the litter was transferred to containers and washed on a sieve (125 μ mesh size) to separate invertebrates from detritus. The remaining plant material was then dried to constant weight at 105 °C. Weight loss was expressed by the equation:

$W_t = W_o e^{-kt}$ (Olson, 1963).

At the beginning of the experiment, and after 15 and 38 days, one subsample of dried leaf litter remaining was analysed in order to determine the changes in the nutrient content.

For total nitrogen, the material was digested in a mixture of hydrogen peroxide and sulphyric acid, and was measured using direct nesslerization and analysed colorimetrically by absorption spectrophotometry.

Total phosphorus was measured according to a vanadomolybdophosphoric yellow colour procedure and cations (Ca, Na, K, Mg) were determined by atomic absorption spectrophotometry. Previously the samples were ashed (4 hours at

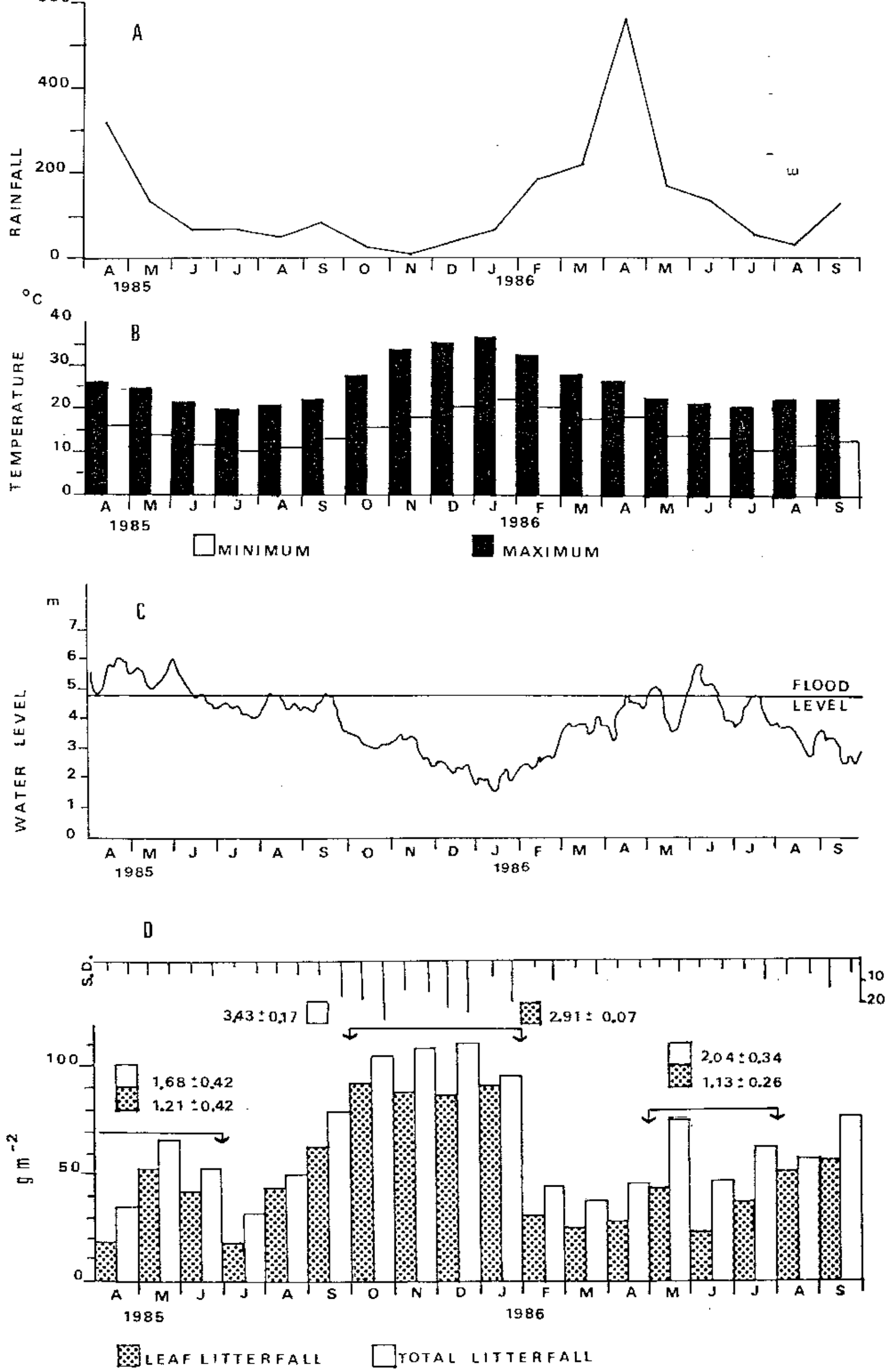

Fig. 1. Monthly total of rainfall (A), mean maximum and minimum daily water temperature (B), water level of Paraná river (C) at Corrientes City, and litterfall of *Tessaria integrifolia* (D) in g m^{-2} d^{-1}. Total litterfall and leaf litterfall for low- and high-water are indicated up the bars. S.D. = standard deviation of total litterfall.

550 °C) and dissolved in HCl. Hemicellulose, cellulose, and lignin fractions were determined after methods used by Goering and Van Soest (1972) for the analysis of forage fiber.

In colonization experiments, nylon litter bags of 5 mm mesh size filled with 10 g of air-dried leaves were used.

Results

The dry weights of the different fractions of *Tessaria integrifolia* litterfall, separated between both high- and low-water phases, are shown in Fig. 1. Annual litterfall in the period April 1985 to March 1986 was 8.15 t ha^{-1}. The average daily values for the same period were 2.23 g m^{-2} of total litterfall of which 79.1% are leaves. Highest leaf fall occurred between October and January when both rain-fall and water level of Paraná river decreased (Fig. 1a, c, d).

During the flooding periods which occurred in April, May and June of 1985; and May, June and July of 1986, lowest daily leaf fall values (approximately 1 g m^{-2}, Fig. 1d) were recorded.

Significant differences were found in the mean dry weight of leaf litterfall between the low- and the high-water phases (ANOVA, $P < 0.05$). These results indicate that leaf litterfall is seasonal with a maximum during the low water and minimum during the high water phase.

The mean weight loss in the first 30 days was 68% (Fig. 2) and the decay coefficient calculated for 38 days was 0.034 (*k* per day). The estimated time for 50% decomposition (half-life) and 95% decomposition was 20 and 88 days, respectively. The real value for 50% decomposition (13 days) was less than the estimate from the model (Fig. 2).

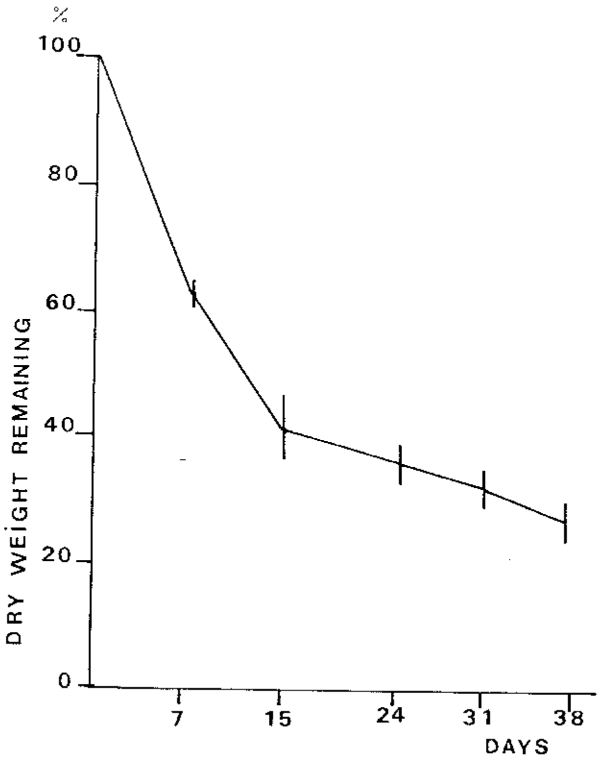

Fig. 2. Remaining dry weight of *T. integrifolia* leaves (in % of original dry weight ± standard deviation of three samples).

Initial concentrations of N, P, K, Mg and Ca of the *Tessaria integrifolia* dead leaves are shown in Table 1. After 38 days of incubation, the order from most rapid to slowest loss of nutrients was: Ca > K > N > Mg > Na > P (Table 1).

The highest mean total number of invertebrates per g remaining litter in the *Tessaria integrifolia*

Table 1. Original composition of *Tessaria integrifolia* dried leaves and changes in content of mineral elements (in % of dry weight) and percent remaining (in % of original amount) during decomposition.

	N	P	K	Na	Ca	Mg
Initial	3.93	0.037	0.48	0.08	2.0	0.14
7 days	3.30	0.035	0.04	0.04	0.94	0.07
% remaining	(83.96)	(94.5)	(8.3)	(50)	(47)	(50)
15 days	2.96	0.036	0.05	0.05	0.82	0.09
% remaining	(73)	(97)	(10)	(62.5)	(41)	(64.2)
38 days	1.51	0.034	0.08	0.04	0.32	0.06
% remaining	(38.4)	(91.8)	(16.6)	(50)	(16)	(42.8)

litter bags was recorded after 30 days of submergence (Table 2). The invertebrates found at different incubation times are also listed in Table 2. The number of collector-gatherers per litter bag increased between incubation days 7 and 38. The number of collector-filterers per litter bag increased during the first 30 days. At 38 days the high suspended silt load (Secchi disk = 4 cm) of Paraná river brought adverse conditions for the collector-filterers.

There was a negative linear correlation between the remaining dry weight of leaves and the number of invertebrates per g remaining litter ($r = -0.90$).

Table 2. Number of individuals per litter bag and per g remaining detritus found in *Tessaria integrifolia* litter bags. The taxa were assigned to functional feeding groups according to Merritt & Cummins (1978).

Incubation days	7	15	24	30	38
Collector–gatherers:					
Chironomidae (larvae)	5	11	12	3.6	7
Campsurus sp. (nymphs)	–	1	2	4.3	10
Tenagobia sp.	–	–	0.3	0.3	–
Oligochaeta (Opistocystidae and *Dero* sp.)	–	–	1	20.6	42
Caenis sp. (nymphs)	–	–	–	1	–
Neotrichia sp. (larvae)	–	10	10	13	6
Subtotal	5	22	25.3	42.8	65
Collector–filterers:					
Cytheridella islovayi	2	2	8	57	10.6
Cyrnellus sp.	–	–	1	1.6	–
Cyclestheria hislopii	–	–	5	12	–
Eupera sp.	–	–	–	0.6	0.3
Subtotal	2	2	14	71.2	10.3
Predators:					
Ablabesmyia sp. (larvae)	9	9	6	15	11
Coenagrionidae (nymphs)	–	–	1.3	0.6	–
B[illegible]a sp. (larvae)	–	–	0.3	0.6	0.6
Dytiscidae (larvae)	–	–	–	0.6	–
Hydracarina	–	–	1	1.3	0.6
Subtotal	9	9	8.6	18.1	12.2
Scrapers:					
Berosus sp. (larvae)	–	–	–	2.6	1
Biomphalaria sp.	–	–	–	0.6	–
Subtotal	–	–	–	3.2	1
*Number of individuals per litter bag	16 ± 3.4	33 ± 9.2	47.9 ± 16	135.3 ± 8	89.6 ± 11.6
*Number of individuals per g remaining litter	2.8 ± 0.5	8.7 ± 2.1	15.1 + 5.0	46.4 ± 7.7	38.0 ± 10.5

*Mean ± standard deviation of three samples.

Discussion

The rate of litterfall in the *Tessaria integrifolia* forest was similar to that of a subtropical floodplain forest of palm reported by Frangi & Lugo (1985), and higher than values obtained for inundation forest of the Amazon river (Franken *et al.*, 1979; Adis *et al.*, 1979), for alluvial forest of North Carolina (Brinson *et al.*, 1980) and for the mean of warm temperature forest (Bray & Gorham, 1964).

High litterfall values may be related to a suitable nutrient availability and high productivity in the floodplain of Paraná river and to the seasonal deficit in soil water supply. The water availability of the soils has been indirectly assessed, since the low water level and low rainfall conditions occurred simultaneously with high temperature. During the study period, flooding was not an important stress factor because of its short duration. However, the effect of a more prolonged inundation periods might be very different. During exceptionally high floods the fringing forest can remain submerged for more than 3 months and the leaves may be completely lost by abscission (Neiff *et al.*, 1985). Thus, several years of observation might be needed to obtain a good estimates of litterfall in such riverine systems. In the temperate zone, a sustantial part of leaf litter input is pulsed in the autumn (Saunders, 1980). In comparison the seasonality of litterfall in the *Tessaria integrifolia* alluvial forest is closely related to the hydrologic regime of Paraná river, with a strong release in low water phase.

A comparison of the data obtained by the litter bag method on the rate of dry weight loss in several species of river forest revels that *T. integrifolia* in the present study decomposes much faster than tree leaves in temperate woodlan stream (Kaushik & Hynes, 1971; Petersen & Cummins, 1974; Sedell *et al.*, 1975; Chauvet, 1987). The k value measured for the decomposition of *T. integrifolia* leaves is greater than that obtained for *Eichhornia crassipes* root litter ($k = 0.010$) and less than that reported for *E. crassipes* leaf litter ($k = 0.063$) incubated simultaneously in Choui Island (Poi de Neiff & Neiff, 1989).

Our preliminary results in the Paraná river do not demonstrate strong dependence of decay rate on initial N concentration. *T. integrifolia* leaves have higher initial N content (Table 1) than *E. crassipes* leaves (Hammerly *et al.*, 1982). A possible alternative explanation of these different decay rates involves lignin: nitrogen ratio (Taylor *et al.*, 1989). The soft texture of *E. crassipes* leaves may be related to low lignin content but, at the present, we have no information on lignin in *E. crassipes*.

Several studies on nutrient release have indicated that cations such as potassium and sodium are the first ones to be lost during decomposition followed by other less labile elements (Howard-Williams & Junk, 1976; Brinson, 1977; Kulshreshtha & Gopal, 1982; Esteves & Barbieri, 1983; Brock, 1984). In our study more potassium (up to 92%) is lost in the first week, whereas 50% of sodium remained until the end of the experiment.

The slowest drop of phosphorus during decomposition should be related with a low content of *P* in a plant tissues, when we compare with other plant litter (Howard-Williams & Junk, 1976; Brock, 1984).

The invertebrate densities on *T. integrifolia* detritus were low when compared with the densities recorded from other studies of tree-leaf and macrophytes decomposition (Richard & Moreau, 1982; Brock, 1984). The small number of associated invertebrates on *T. integrifolia* litter could result from the low N availability associated with a poor microbial activity.

After 38 days of incubation, the number of individuals per g remaining litter in *T. integrifolia* was less than *E. crassipes* leaves (Poi de Neiff & Neiff, 1989). It is apparent that different species of leaves support very different densities of invertebrates, and that higher densities of invertebrates occur on those leaves which decompose most rapidly (Hart & Howmiller, 1975; Richard & Moreau, 1982; Petersen, 1984).

Species which are abundant in the deep water layers leaf of samples of central amazonian inundation forest (Irmler & Junk, 1982), like Oligochaeta, Chironomidae and *Cyclestheria hislopii* are found in the *T. integrifolia* litter.

The fine particle feeders or collectors were the most abundant of all invertebrates in *T. integrifolia* litter. There were no shredders colonizing the leaf litter bags. A similar finding was noted for *E. crassipes* litter (Poi de Neiff & Neiff, 1989). In contrast, Seddell *et al.* (1975); Cummins *et al.* (1972) and Richard & Moreau (1982) found that shredders are important in various temperate streams. Paraná river is much larger than any of these streams and does not have at Choui Island an invertebrate community functioning as large particulate organic feeders. According to Vannote *et al.* (1980) with increasing stream size and re[illegible]tion in detrital particle size, collectors should increase in importance and dominate the macroinvertebrate assemblages of large rivers.

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