Journal of Tropical Forest Science 14(2): 223–233 (2002)

LITTER DECOMPOSITION AND NUTRIENT RELEASE IN A SUBTROPICAL FOREST OF ARGENTINA

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Received October 2000

PALMA, R. M., PRAUSE, J., EFFRON, D., DE LA HORRA, A. M. & GALLARDO LANCHO, J. F. 2002. Litter decomposition and nutrient release in a subtropical forest of Argentina. The aims of this study were to determine the litter decomposition rate, the release dynamic and return to the soil of the N, P and K nutrients coming from four native species, namely, espina corona (*Gleditsia amorphoides*), guayaibí (*Patagonula americana*), mora (*Chlorophora tinctoria*) and urunday (*Astronium balansae*) in a subtropical forest of Argentina, during one year. Litter decomposition and nutrient release were fitted either to a double exponential model and/or to a simple exponential model in order to find the best fit. Espina corona produced the greatest amount of litter, had the greatest initial amounts of N, P and K and decomposed rapidly. These traits indicated that espina corona played a major role in nutrient cycling in the subtropical moist forest of the Estricta Natural Reservation. Following espina corona, and in decreasing order, mora released more nutrients, and guayaibí and urunday gave considerably smaller nutrient concentrations. Differences in litter decomposition or release rates of nutrients to the soil from different leaf litter types reflect the complexity of the decomposition and release processes. This was confirmed by the fact that both litter decomposition and nutrient release followed different mathematical models according to the species. It is important to note that the species diversity allows a natural ecosystem to maintain its fertility and nutrient balances.

Key words: Litter bags - subtropical forest - leaf litter decomposition - rate decomposition - nutrient release

PALMA, R. M., PRAUSE, J., EFFRON, D., DE LA HORRA, A. M. & GALLARDO LANCHO, J. F. 2002. Pereputan sarap dan pelepasan nutrien di hutan subtropika Argentina. Tujuan kajian adalah untuk menentukan kadar pereputan sarap, dinamik pelepasan dan pemulangan kepada tanih bagi nutrien N, P, dan K daripada empat spesies asli iaitu corona (*Gleditsia amorphoides*), guayaibí (*Patagonula americana*), mora (*Chlorophora tinctoria*) dan urunday (*Astronium balansae*) di hutan subtropika Argentina dalam tempoh setahun. Pereputan sarap dan pelepasan nutrien dipadankan sama ada dengan model eksponen berganda dan/atau dengan model eksponen mudah bagi mendapatkan padanan yang terbaik. Espina corona menghasilkan jumlah sarap yang paling banyak, mempunyai jumlah awal N, P dan K yang paling banyak dan mereput dengan pantas. Ciri-ciri ini menandakan bahawa espina corona memainkan peranan penting dalam kitaran nutrien di hutan lembap subtropika di Estricta Natural Reservation. Menyusuli espina corona dalam susunan menurun, mora membebaskan lebih banyak nutrien, manakala guayaibí dan urunday membebaskan kepekatan nutrien yang lebih sedikit. Perbezaan kadar pereputan sarap atau pembebasan nutrien daripada jenis sarap daun yang berbeza ke atas tanih menunjukkan kerumitan proses pereputan dan pembebasan. Ini disahkan oleh kenyataan bahawa kedua-dua pereputan sarap dan pembebasan nutrien mengikut model matematik yang berbeza menurut spesies tertentu. Kepelbagaian spesies membolehkan ekosistem semula jadi mengekalkan kesuburan dan keseimbangan nutrien.

Introduction

Cycling of nutrients is a fundamental component in the functioning of forest ecosystems. The majority of nutrients required for plant production are made available through the decomposition of litter (Waring & Schlessinger 1985). The presence of litter represents a provisional accumulation of elements which are gradually released, ensuring the permanent contribution of nutrients to the soil (Hernández *et al.* 1992). In some tropical forests, a greater part of the nutrient reserves are found in the plant biomass, compared with in the soil (Godeas *et al.* 1985).

Different types of plant litter have chemical compositions that are characteristic of each species (Prause 1997). Nutrients in the leaf litter are rapidly mineralised and absorbed by the roots in the rainy season (Martín *et al.* 1994). Litter decomposition and nutrient mineralisation can potentially set up a positive feedback cycle between nutrient mineralisation and litter quality (Edmonds *et al.* 1990). However, Keenan *et al.* (1996) argued that feedback is controlled by the extent to which different species can withdraw nutrients at the time of leaf senescense. Plant nutrients are released from litter either by physical leaching or by break down of structural organic components by soil organisms. Often the later process is quantitatively more important, and the rate at which elements are released could thus be expected to be governed largely by the rate of decomposition (Staaf 1980, Cornejo *et al.* 1994).

The aims of this study were to determine the leaf litter decomposition rate, the release dynamic and return to the soil of the N, P, and K nutrients for four native species in a subtropical forest of Argentina, during one year.

Materials and methods

The study site is a subtropical moist forest located at the Estricta Natural Reservation (27–28° S, 57–60 ° W) in Colonia Benitez, Chaco Province, Argentina. This reservation has been declared a national interest in order to preserve sites of great biological value that are in danger of extinction. Annual average precipitation is 1300 mm, with a mean annual temperature of 21.5 °C.

The soil is classified as Oxic Argiudoll (Ledesma & Zurita 1995) and has the following characteristics: oxidisable C = 50 g kg^{-1}, total N = 4 g kg^{-1}, available P = 51 mg kg^{-1}, available Ca = 2500 mg kg^{-1} and pH 6.3 (soil: water ratio = 1:2.5), with a loamy silt texture.

In this polyphytic forest, 10 one-hectare (100 × 100 m) plots were selected to represent an ecosystem relatively uniform in soil and vegetation. In each plot, one tree of the four dominant species in this forest were selected. The species were:

(1) Espina corona (*Gleditsia amorphoides*): family Leguminosae, tree of 15–18 m height and diameter at breast height (dbh) 55–65 cm. This tree, which has an excellent veined wood, is widely spread over the humid formations in the north of Argentina.

(2) Guayaibí (*Patagonula americana*): family Borraginaceae, tree of 18–20 m height and dbh 60–75 cm. This species is widely spread over Parque Chaqueño Oriental and Selva Misionera.

(3) Mora (*Chlorophora tinctoria*): family Moraceae, tree of 18–20 m height and dbh 40–50 cm. It provides one of the most beautiful native woods. It is typical of Parque Chaqueño Oriental and the Selva Tucumano-Oranense.

(4) Urunday (*Astronium balansae*): family Anacardiaceae, tree of 18–25 m height and dbh 60–70 cm. It is a typical species of Parque Chaqueño Oriental.

The vegetation in these plots was very uniform in height, in spite of moderate variation in dbh. All the selected trees showed no evidence of growth abnormalities and damage. Sample extractions and field measurements were carried out between September 1997 and September 1998.

Litter fall was collected in three circular plastic traps, each measuring 1 m^2 with a 2-mm mesh size. The traps were hung randomly at 0.5 m above the ground under each selected tree. Total litter was collected monthly for one year. The leaf litter from each of the selected species was oven-dried at 70 °C and weighed to determine the leaf litter production.

Litter decomposition was studied using the litter bag technique. This method allowed the determination of litter mass loss in the field and the subsequent chemical and biological examination of the residual material. This technique is frequently used to obtain information on simultaneous comparisons of different species at the same experimental site, especially under field conditions (Wieder & Lang 1982, van Wesemael 1993).

Thirty grams of leaf material were placed in 30 × 30 cm plastic bags with a mesh size of 2 mm so as not to exclude the activity of the mesofauna (Swift *et al.* 1979). Mesh with larger openings was not used in order to avoid the risk of physical loss of the confined plant material (Martín *et al.* 1997). On 21 September 1997, 160 bags were placed on the soil surface, four bags each under espina corona (EC), guayaibí (GY), mora (MR) and urunday (UR). Every three months, one bag from under each species in each plot was randomly collected. The collection dates were 21 December 1997, 21 March 1998, 21 June 1998 and 21 September 1998.

The samples obtained were oven-dried at 70 °C. Dry mass was determined and the following determinations were carried out: N by the micro-Kjeldahl method, P by colorimetry with ammonium metavanadate (Chapman & Pratt 1979) and K by flame photometry. The last two nutrients were determined after wet digestion of the plant material with a mixture of perchloric and nitric acids (1:5 v/v).

The released mass percentages ($\% R_t$) by the litter bags were calculated from the mass of leaf litter (M_t) at each sample period of time (t) and the initial mass (M_0), according to the following equation:

$$\% R_t = \frac{M_0 - M_t}{M_0} \times 100$$

The released mass of each nutrient (R_X) was calculated in the same way:

$$\% R_x = \frac{X_0 - X_t}{X_0} \times 100$$

where X represents the mass of N, P or K at the beginning (X_0) and at time t (X_t).

Decomposition of leaf litter and nutrient release were fitted to the simple exponential function (Olson 1963) and/or the double exponential function (Bunnel & Tait 1974), in each case selecting the model with the best fit.

The simple expotential function was represented by the following equation:

$$\ln (X_t/X_0) = - k\, t$$

where k = a constant of decomposition.

The double exponential function was represented by the equation:

$$w_t = w_l \exp(- p_l\, t) + w_r \exp(- p_r\, t)$$

where:

w_t = final mass of the leaf litter or the final mass of each of the nutrients,
w_l = initial mass of the leaf litter or the initial mass of each of the nutrients in the easily decomposable compounds,
w_r = initial mass of leaf litter or the initial mass of each of the nutrients in the compounds more difficult to decompose,
p_l = the constant of loss of mass of leaf litter or of nutrients (representing the easily decomposable components) and
p_r = the constant of loss of mass of leaf litter or the constant of loss of mass of nutrients (representing the more recalcitrant components).

The values of w_r were obtained by fitting the points corresponding to 3, 6, 9 and 12 months to a straight line. The point of interception on the *y*-axis is w_r and the slope of this line is p_r; w_l was calculated according to the difference:

$$w_l = 100 - w_r$$

The return of nutrients to the soil (X_{return}) coming from the leaf litter was calculated as:

$$X_{return} = \frac{[X_0] \times LLP \times R_x}{100}$$

where:

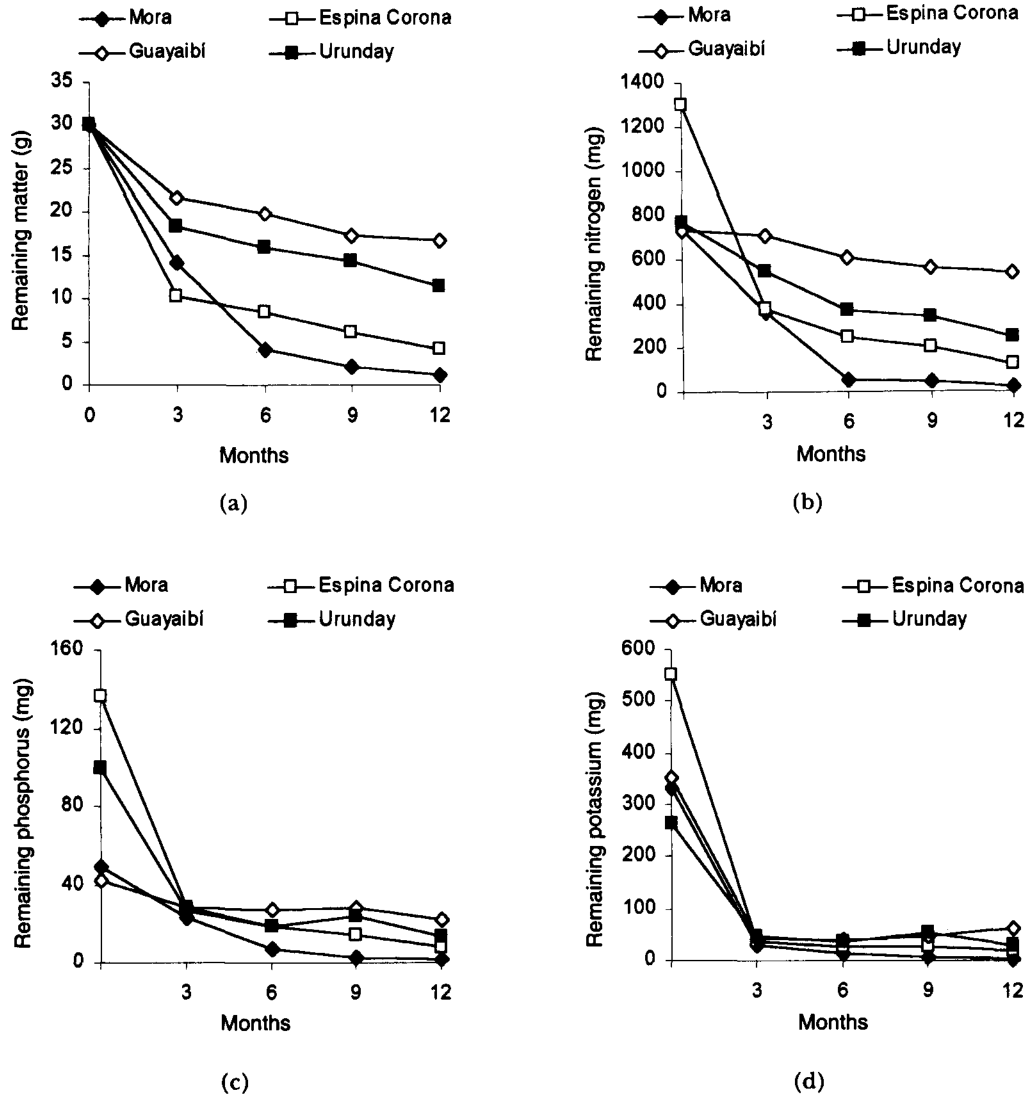
$[X_0]$ = initial leaf litter concentration of each nutrient,
LLP = leaf litter production,
R_x = released mass of each nutrient.

Prior to analysis of variance, the normality of the data of all the variables as well as the homogeneity of variance was checked using Levenne's test. The Tukey-Kramer test was used to detect differences among the means. Equations were established for each of the models mentioned.

Results and discussion

Mass loss

Figure 1a shows the absolute mass content of residual plant matter in the litter-bags. The two species that contributed a greater amount of leaf litter to the soil, EC and MR, also showed more rapid leaf decomposition, differing significantly from the values for GY and UD (Table 1). These differences can be explained by the different chemical composition of the plant material that, among other factors, influences the decomposition rate (Ballini & Bonin 1995). Over 80% of the dry matter in EC and MR was mineralised at the end of the year, in contrast with only 46% in CY.



(a) (b)

(c) (d)

Figura 1 Remaining matter of leaf litter (a), remaining nitrogen mass (b), remaining phosphorous mass (c) and remaining potassium mass (d) at three-month intervals over the course of decomposition in September 1997 – September 1998, by species.

Table 1 Initial leaf concentration of nutrients, percentages of decomposition of dry matter and nutrient release (in 1 year), litter production and nutrient return to the soil

	Espina corona	Guayaibí	Mora	Urunday
Initial leaf concentration of nutrients (mg g^{1})				
N initial concentration	43.1a	24.4b	24.8b	25.7b
SD (±)	3.2	2.7	1.9	2.2
P initial concentration	4.5a	1.4b	1.6b	3.3ab
SD (±)	0.4	0.1	0.1	0.2
K initial concentration	17.4a	11.8b	11.1b	8.8c
SD (±)	1.2	1.0	0.9	0.7
Percentages of decomposition: dry matter and nutrient release (after 1 year)				
Dry matter decomposition (%)	85.9b	45.9d	95.4a	61.9c
SD (±)	8.7	5.0	10.2	5.9
Released N (%)	90.9a	26.4c	96.9a	66.6b
SD (±)	8.0	3.2	9.7	7.1
Released P (%)	93.9a	46.7c	95.9a	86.7b
SD (±)	9.2	5.0	9.6	9.0
Released K (%)	95.9a	80.8b	98.9a	88.2b
SD (±)	9.1	8.0	10.0	9.1
Leaf litter production and nutrient return to the soil (kg ha^{-1} yr^{-1})				
Leaf litter production	1095a	373b	931a	249b
SD (±)	55.6	46.3	52.8	29.1
N return	42.8a	2.4c	22.3b	4.3c
SD (±)	4.5	0.3	1.9	0.3
P return	4.6a	0.2c	1.4b	0.7c
SD (±)	0.5	0.02	0.1	0.03
K return	18.4a	3.6c	10.2b	1.9c
SD (±)	1.7	0.4	0.9	0.2

Different letters indicate significant differences ($p < 0.05$) between means of the different species. SD (±) means standard deviation.

The decomposition rate decreased over time, although not all the species showed the same pattern of decomposition. EC, GY and UD showed two stages of leaf litter decomposition, each one with a different constant of decomposition. The recalcitrant fraction was much greater for GY and UD (about 75%) than in the other two species. The first stage was a rapid process which took place during the first trimester, corresponding to the decomposition of the more labile components. Similar results were found by Hernández *et al.* (1992), Wild (1992) and Santa Regina *et al.* (1997). The second stage was much slower and was associated with a more resistant fraction. Owing to this behaviour, the decomposition rate (Table 2) was described by the sum of two exponential functions. Unlike the other three species, the decomposition constant of MR showed a better fit to the simple exponential model; the decomposition constant was close to 0.30, which is similar to that for many temperate zone litters (Martín *et al.* 1997).

Nitrogen

Figure 1b shows the N content remaining in the bags. At the beginning of the study EC had the highest concentration of N in the leaves, possibly because of its high capacity for biological fixation since it is one of the Leguminoseae. EC showed rapid release of N during the first trimester as a consequence of microbiological activity, which was detected through a high respiration index (Palma, pers. comm.). After the third month, the N remaining declined so slowly that differences were not statistically significant ($p < 0.05$). The other tree species showed concentrations of N similar to each other at the beginning, but with different release rates. GY had the slowest N mineralisation and almost all its N remained in the organic residue.

N release dynamic showed the same model as that of leaf litter decomposition for EC and MR (Table 2). In contrast, the single exponential model best described the N release data for GY and UD whereas the double exponential model best fit the mass loss data.

Table 2 Relationships between leaf litter decomposition, nutrient release and time (t) in the different tree species

Production	Equation	r^2
Espina corona		
Remaining dry matter	$y = 49.4 \exp(-1.30\,t) + 50.6 \exp(-0.11\,t)$	0.99**
Remaining N	$y = 57.4 \exp(-1.35\,t) + 42.6 \exp(-0.12\,t)$	0.99**
Remaining P	$y = 67.8 \exp(-1.40\,t) + 32.2 \exp(-0.14\,t)$	0.99**
Remaining K	$y = 91.8 \exp(-1.51\,t) + 8.2 \exp(-0.07\,t)$	0.99**
Guayaibí		
Remaining dry matter	$y = 22.1 \exp(-1.03\,t) + 77.9 \exp(-0.029\,t)$	0.99**
Remaining N	$y = 100 \exp(-0.032\,t)$	0.95**
Remaining P	$y = 88.3 \exp(-0.044\,t)$	0.77**
Remaining K	$y = 88.5 \exp(-1.46\,t) + 19.4 \exp(-0.008\,t)$	0.98**
Mora		
Remaining dry matter	$y = 100 \exp(-0.29\,t)$	0.99**
Remaining N	$y = 87.8 \exp(-0.30\,t)$	0.92**
Remaining P	$y = 95.9 \exp(-0.28\,t)$	0.98**
Remaining K	$y = 79.4 \exp(-0.36\,t)$	0.91**
Urunday		
Remaining dry matter	$y = 28.2 \exp(-1.11\,t) + 71.8 \exp(-0.05\,t)$	0.99**
Remaining N	$y = 94.3 \exp(-0.089\,t)$	0.97**
Remaining P	$y = 63.7 \exp(-1.31t) + 36.3 \exp(-0.071\,t)$	0.95**
Remaining K	$y = 81.3 \exp(-1.47\,t) + 18.62 \exp(-0.041\,t)$	0.99**

** $p < 0.01$, $n = 10$

Although N forms part of the structure of organic matter and it is only released when the heterotrophic microorganisms consume C, the different rates of N release are regulated by the different organic components of the leaf material of the forest species (Ballini & Bonin 1995).

Analysis of the percentages of released N (% R_N) showed that MR released more N at the end of the study period, followed by EC, UD and, finally, GY (Table 1). These values can be related to the resistance showed by the nitrogenated compounds to be released by microorganisms from organic matter. On the other hand, it has also been reported that the N contents first increased before they are gradually released, and this increment is attributed to new nitrogen supplies by the leachates of the tree canopy or atmospheric deposition (van Wesemael 1993, Santa Regina *et al.* 1997).

Phosphorus

Figure 1c shows the P contents remaining in the bags. The plant species with higher initial concentrations of this element were EC and UD. They also showed rapid release of P during the first trimester but remained almost constant for the rest of the study ($p < 0.05$). GY and MR had lower concentrations and release rates than EC and UD. Also MR had lost almost all the P by the end of the year (Table 1).

P is part of the organic matter in plant tissue. Its release model for the EC, MR and UD species was the same as that followed by the leaf decomposition (Table 2). However, the same did not occur for GY which showed double exponential model for leaf litter decomposition and simple exponential for P. The labile fraction for this nutrient is much more abundant (65%) than the resistant one (35%) in EC and UD (Figure 1c).

Analysis of the percentages of released P after a year, revealed that MR and EC released most of their P, followed by UD and, finally, GY (Table 1). This order is the same as that followed by N release. In contrast, as in the case of N, it has also been reported that P accumulates in leaf litter during the first year of decomposition owing to new supplies by the leachates of the tree canopy or atmospheric deposition (van Wesemael 1993).

Potassium

Figure 1d shows the K contents remaining in the litter bags. EC was the species with the highest initial concentration, as it was for N and P.

There was a strong K release during the first trimester in all the species studied. This coincides with the findings of Ballini and Bonin (1995) and is due to the high solubility of this element. This behaviour can be attributed to the fact that, in general, K does not form part of the organic structure of the leaf litter and is susceptible to losses through leaching (Staaf 1980, Waring & Schlesinger 1985). K release in the four species followed a model similar to that followed by the leaf litter decomposition, but the slopes of the labile fraction are significantly greater ($p < 0.05$) for K release than for mass loss (Table 2). The labile fraction exceeded 80% in EC, GY and UD.

When percentages of released K were analysed at the end of the assay, MR was the species that showed the highest release rate, followed by EC, UD and GY (Table 1).

Nutrient return to the soil

Table 1 shows the nutrient return to the soils which depended on three factors: aboveground production, initial composition of the leaf litter and the release rate of each nutrient (Gallardo *et al.* 1995).

EC showed the greatest initial concentration of nutrients, the greatest contribution of leaf litter and the highest release rate (Table 1). Consequently, it supplied the greatest amount of nutrients to the soil. In decreasing order, it is followed by MR, which showed high decomposition rate, high aboveground production, but low initial concentration of nutrients. GY and UD showed the lowest contribution of leaf-litter and the lowest release rate but similar initial concentrations to MR; therefore, they showed low return of nutrients during the studied period (Table 1).

Initial concentrations of N and P in the plant material are important for the decomposition of the leaf litter because of their influence on microbial activity (Taylor *et al.* 1989, Gallardo *et al.* 1997). Correlation between the initial concentration of these nutrients and the mass loss for the tree species (not shown), indicated significant relationships for N and P only when MR was excluded from the analysis, since this species differed in its decomposition model (simple exponential) from the others. For EC, GY and UD, the correlation coefficients between the above mentioned variables were $r = 0.93$ for N ($p < 0.001$) and $r = 0.98$ for P ($p < 0.001$).

Differences in release rate of nutrients to the soil from different leaf litter types indicated the complexity of the decomposition and release processes. This was confirmed by the fact that nutrient release followed different mathematical model according to the species. It is important to note that the species diversity allows a natural ecosystem to maintain its fertility and nutrient balances.

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