

LEAF LITTER QUALITY AND LITTER DECOMPOSITION OF WOODY SPECIES IN A SEASONAL SUBTROPICAL FOREST (ARGENTINA)

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Abstract. The objective of this paper is to determine the relationship between leaf litter decomposition rate and leaf attributes in different subtropical seasonal forest microsites. We studied the litter decomposition of two trees and two shrub species of the *Schinopsis balansae* forest (quebrachal) in the Chaco Region of Argentina. Decomposition was studied using the bag method. Leaf density, volume, and leaf/perimeter area ratio were measured. We also determined the amount of organic matter, ash, nitrogen, potassium, calcium, and magnesium present in leaves, as well as fiber, lignin, cellulose, and hemicellulose concentration. Results were adjusted to monophasic decomposition with a remaining weight decay model. Morphological characteristics do not show any influence on decomposition rates. The influence of shade is small. Apparently, nitrogen concentration does not control litter decomposition in this humid Chaco Region forest, except in the case of *Acacia praecox*. Species with the highest decomposition rate also bear leaves with the highest nutrient concentration (*Achatocarpus praecox* and *M. vitis-idaea*). The decomposition rates of species analyzed in this paper did not follow a common pattern. Accepted 16 January 2009.

Key words: *Acacia praecox*, *Achatocarpus praecox*, carbon dynamics, Chaco, litter decomposition, *Maytenus vitis-idaea*, nutrient concentration, secondary compounds, *Schinopsis balansae*, woody species.

INTRODUCTION

The carbon dynamics of an ecosystem is the result of assimilation through plant photosynthesis, the deposition, decomposition, and incorporation of litter into the soil, and the dissipation of carbon as carbon dioxide into the air or its storage as organic matter in the soil. Organic matter production rate, plus carbon and nutrient availability and recycling capacity are different for each species and can be quantified (Proctor 1983, Montagnini *et al.* 1993). Nutrient cycling, as well as carbon dynamics, are essential for the functioning of the ecosystem. Human activity modifies carbon accumulation in the soil while management practices can increase carbon concentration in any ecosystem, more significantly in forest ecosystems (Lal *et al.* 2003). Litter decomposition determines the potential of forest soils for atmospheric carbon sequestration (Jurgensen *et al.* 2004), and it is one of the biological indicators in determining soil quality (Knoepp *et al.* 2000).

Determining the decomposition rate allows us to assess the humification process that involves the conversion of biomass into humic substances that are relatively resistant to microbial decomposition and have a long turnover time. This is one of the pedogenic processes in carbon sequestration (Lal *et al.* 2003).

Environmental conditions influence the physical and chemical characteristics of the fallen material, regulating the rate of nutrient liberation from organic matter (Facelli & Pickett 1991). Temperature, moisture, and soil aeration may influence litter decomposition, conditioning microbial and mesofaunal activity (Santa Regina *et al.* 1989, Martin *et al.* 1994, Knoepp *et al.* 2000). Other variables in litter decomposition are the characteristics of dry matter determined by different C/N ratios and levels of lignin (Van Soest & Wine 1968, Hobbie 1992, Velazco *et al.* 1992–1993, Gallardo & Merino 1993, Montagnini *et al.* 1993, Coûteaux *et al.* 1995, Cornelissen & Thompson 1997, Heal *et al.* 1997, Sariyildiz 2003).

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Therefore the substrate quality may be different depending on the species (Berg 1998), producing different conditions for the soil fauna of the site. While C/N ratio is considered a general index of substrate quality, the relative importance of the chemical and physical components of dry matter has not yet been assessed (Heal *et al.* 1997, Sariyildiz 2003). The nutrient level of litterfall, and therefore the composition of organic matter, is determined by two factors: the mineral level of the component tissues, and the season and manner in which they fall, i.e. leaves falling individually or massively and synchronously in a specific season (Lousier & Parkinson 1975).

In the Chaco Region forests where this study was carried out, the canopy is not homogeneous. In typical Natracualfs soils, some sections present a dense tree layer, while in depressed or udolic Ocracualfs soils there is either an open canopy or no trees at all (Mussetti & Alconchel 1986). This mosaic of soils, together with the vegetation, creates different microsites that can influence the decomposition of litter in different ways.

Litter decomposition rate has been analyzed in different types of forests, tropical forests (Singh 1992, Cuevas & Lugo 1998, Alvarez-Sanchez & Becerra Enríquez 1996), deciduous forests of the boreal region (Swift *et al.* 1979, Stump & Binkley 1992, Keenan *et al.* 1996), and recently in works about the decomposition of two species in the humid Chaco Region forest in Argentina (Prause *et al.* 2002, 2003).

The aim of this paper is to determine the relationship between the leaf litter decomposition rate and the characteristics of the leaves of four species in microsites within the humid Chaco Region forest. It is also important to determine the amount of time needed for litter nutrients to become available again in the system in order to establish proper forest management practices.

The hypotheses are:

H₁. The litter decomposition rate on the forest ground depends on the environmental characteristics of the microsite.

H₂. The litter decomposition rate depends on leaf morphology and chemical constituents.

Methods

Study area. Gran Chaco is one of the largest phytogeographical units in the neotropical region and includes central northern Argentina, western Paraguay,

southeastern Bolivia, and a small area in southern Brazil, comprising approximately 1,000,000 km² from 15° to 35° S. Most authors identify a humid area in the east and a dry area in the west (Ragonese & Castiglione 1947, Cabrera & Willink 1980). To the south of the eastern Chaco Region is the Santa Fe Forest Wedge where we find several types of seasonal forests with different elevation and moisture gradients, the most important being the *Schinopsis balansae* forests (quebrachal) (Lewis & Pire 1981). Our research was carried out at Las Gamas Ministry of Agriculture Experimental Center, near the city of Vera (29°28'S, 60°28'W) in the Santa Fe Forest Wedge. This area was heavily lumbered in the past, but it has been partially reforested and it is currently used for cattle grazing and some wood extraction. The most important tree species are *S. balansae*, *Acacia praecox*, and shrubs (Lewis *et al.* 1997). The climate is seasonal subtropical and annual rainfall varies between 800 and 1300 mm. Mean annual temperature is 18°C, with an absolute maximum of 48°C and an absolute minimum of -5°C (Burgos 1970). Land relief varies from gentle slopes to flat plains and small depressed areas. Soil distribution is related to topographic elevation, and the more depressed areas are not well drained. The soils are typical Natracualfs, or udolic Ocracualfs (Mussetti & Alconchel 1986), with a high salt content (Table 1). These forests, called *quebrachales*, suffer droughts during the winter and regular floods in the autumn and spring.

Microsites were defined according to microrelief, soil humidity, and the presence of bromeliads and then classified as dry plain (PS), humid plain (PH), concave (C), convex with bromeliads (EB) (Barberis 1998). After a rainfall, the humid plains and the concave microsites remained flooded for a longer period of time. Five microsites received plenty of sunlight and five were under canopy shade.

Data collection. Litter decomposition was analyzed using the litter bag method in order to compare species and different field conditions (Wieder & Lang 1982). Leaves were collected from trees and shrubs in mid-autumn (May, 1997) when they normally start to fall. Leaves were chosen from three individuals of four species: two trees, *S. balansae* and *Acacia praecox*, and two shrubs, *M. vitis-idaea* and *Achatocarpus praecox*. All samples were collected on the same day. Leaves were oven dried at 60°C for 48 hours, then 10 g of dry material were placed in a 1 mm nylon mesh 20 × 20 cm bag. Twenty-four bags

TABLE 1. Organic matter (%), pH and cations (meq/100 g) of Typical Natraqualf and Udolic Ochraqualf

Soils	Typical Natraqualf			Udolic Ochraqualf		
	A2	B21	B3	Ap	B21	B3
Horizon	A2	B21	B3	Ap	B21	B3
Thickness (cm)	0-10	10-25	68-69	0-10	10-25	63-82
Organic Matter (%)	7.14	4.1	0.46	1.51	1.56	0.48
Total Nitrogen (%)	0.33	0.21	0.056	0.10	0.08	0.054
Sodium (cmol.Kg-1)	2.45	4.45	2.3	2.1	2.6	2.6
Calcium (cmol.Kg-1)	14.02	17.31	19.8	14	15.4	23.6
Potassium (cmol.Kg-1)	1.62	1.67	0.7	1.1	1.3	0.6
Magnesium (cmol.Kg-1)	5.1	7.12	2.6	6.4	4.6	2.8
pH	6.4	7.2	8.2	7.3	7.4	8.4

containing one of the four species were distributed on the ground in each microsite.

A two-factor experimental design was established. One of the factors was microsite characteristic (dry plain, humid plain, concave, convex with bromeliads), and the other was exposure to sunlight (full sunlight or canopy shade). Therefore there were 96 bags per microsite, making a total of 960 samples.

Analysis of leaf physical and chemical characteristics.

The physical characteristics of leaves vary according to species. *Schinopsis balansae* leaves are oblong-lanceolate, 4 to 8 cm long by 1.5 to 2 cm wide, showing a smooth, slightly undulated border, rounded and glabrous at the base, with a membranous or slightly leathery texture (Libro del árbol, 1975). *Acacia praecox* leaves, are bipinnate with 3 to 5 pairs of 6 to 11 cm long leaflets, and slim (Burkart 1987). *Achatocarpus praecox* leaves are elliptical or ovate with an acute to obtuse apex sometimes mucronate, glabrous, with a membranous texture (Burkart 1987). Leaves of *M. vitis-idaea* are 1.9 cm long, fleshy, obovate, with a smooth or slightly indented border (Cabrera 1976).

Leaf density (g/mm^3), volume (mm^3), and perimeter/area ratio were measured in the laboratory. Leaf area was determined by means of an "L1-3100-area Meter". Volume was determined by the amount of liquid displaced. The perimeter was determined by a curvimeter with a graded scale. Data were calculated from 40 leaves (leaflets in the case of *Acacia praecox*) from each of the species. Leaf tissue organic matter, ash, total nitrogen, potassium, calcium and magnesium were determined in the four species analyzed. Leaves were collected in autumn and spring from three individuals of each species in order to determine whether there was nutrient translocation

before leaf fall. Organic matter was calculated by weight loss after ignition at 500°C in a muffle. Mineral nutrients were determined by dissolving the ash in hydrochloric acid, potassium by flame photometry, and calcium and magnesium with the Varsene titration procedure. Phosphorus compounds were converted into phosphates, which together with sulfonic acid form a blue precipitate of phosphomolybdate, then phosphorus was determined with a photo-colorimeter. Nitrogen was determined using the Kjeldahl method (Jackson 1964).

Fiber was observed in three compound samples of the analyzed species. Each compound sample was collected from five different individuals in autumn. Fiber percentage of leaves was measured in neutral detergent fiber and in acid detergent (Komarek 1994), as was lignin, cellulose and hemicellulose (Van Soest & Wine, Goering & Van Soest 1970).

Data analysis - Morphology. Data deviations from the regression line were calculated with 5% of confidence interval for leaf density (g/mm^3), volume (mm^3), and perimeter/area ratio.

Chemical characteristics - Fiber and lignin. A multiple-comparison test was used to determine significant differences ($p < 0.5$) between the average nutrient contents of each species. The method employed to discriminate among the means was Fisher's least significant difference (LSD) procedure. Two factors analysis of variance was used to measure nutrient contents in autumn and spring.

Decomposition rate of organic matter. Data from the litter replicas collected at each microsite showed average rates. The loss of organic matter was calculated considering the difference between initial

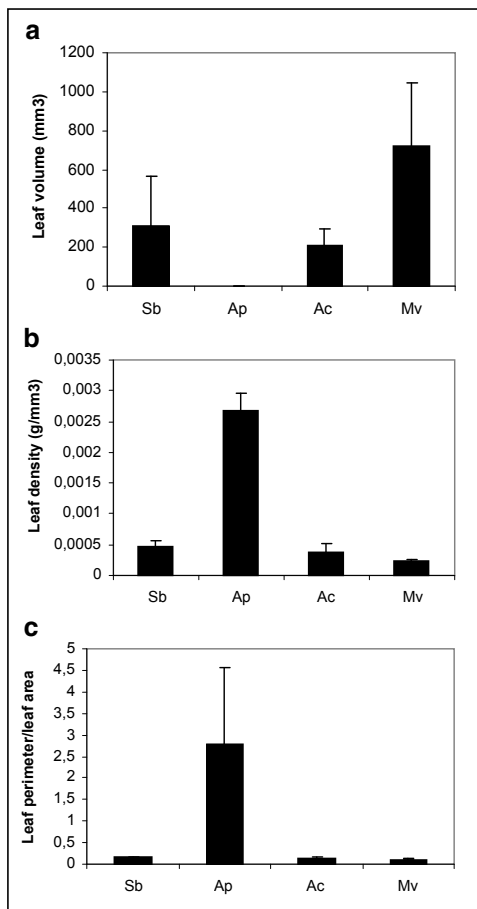


FIG. 1. Leaf morphological characteristics. a. Leaf volume of the species; b. Leaf density of the species; c. Leaf perimeter/area ratio of the species.

References: Sb = *Schinopsis balansae*; Ap = *Acacia praecox*; Ac = *Achatocarpus praecox*; Mv = *Maytenus vitis-idaea*.

weight ($W_0 = 10$ g) and weight at time t (W_t) the remaining weight percentage W was equal to $100W_t/W_0$.

To calculate the decomposition rate, three different models were employed; the best adjusted was the monophasic decomposition model with remaining weight (Carnevale 2000). In this model, leaf litter is decomposed at a constant rate, but as decomposition is not complete, there is an amount of litter remaining that has not been completely decomposed at the end of the process. Decomposition curves of each species at different microsites were compared, using

Graph Pad Prism version 2.0 (GRAPHPAD Software, San Diego, California, USA, www.graphpad.com).

The model equation adjusting to the data is

$$W_t = \text{span} * e^{-kt} + \text{plateau} \text{ or } W_t = \text{Initial weight} - \text{Remaining weight}$$

$$W_t = \text{Decomposed fraction} * e^{-kt} + \text{Remaining fraction}$$

The Prism program can also compare different segments of the curve, i.e. span, k , and plateau. Two factor (species and microsites) variance analysis were used for data comparisons. Microsites with plenty of sunlight were divided (according to their topographic location) into dry plain, humid plain, and convex, and shaded microsites into elevated with bromeliads and concave. Dunn's multiple comparison test was employed.

For each species, the decomposition rates at these microsites were correlated with the nutrients and fiber contents, applying randomized linear regression (Manly 1996, 1997).

RESULTS

Leaf morphology. Fig. 1 shows that *M. vitis-idaea* leaves were the most voluminous, *Acacia praecox* leaflets had the highest density and their perimeter/area ratio was notably higher than the other species analyzed. Of all morphological characteristics analyzed, only density was related with decomposition.

Leaf chemical characteristics. The most important differences between two species were in the amount of ash, C, Ca, Mg, and K. The shrub species (*Achatocarpus praecox* and *M. vitis-idaea*) showed a higher amount (%) of Ca and Mg than the tree species. *Achatocarpus praecox* showed the highest amount of K of all the species, while *S. balansae* showed a significantly higher amount of P and N content.

Significant differences between autumn and spring concentrations of different elements in the species could not be detected by statistical analysis, nevertheless their absolute values showed some seasonal differences (Fig. 2).

Leaf fiber and lignin average. The percentage of leaf fiber, lignin, total N, and the average values of lignin/N and C/N in the four species are shown in Table 2. Among them, the highest lignin/nitrogen ratio corresponded to *M. vitis-idaea*, but the relationship between decomposition rate and lignin/N was not significant. The highest total nitrogen concentration was found in *Acacia praecox*.

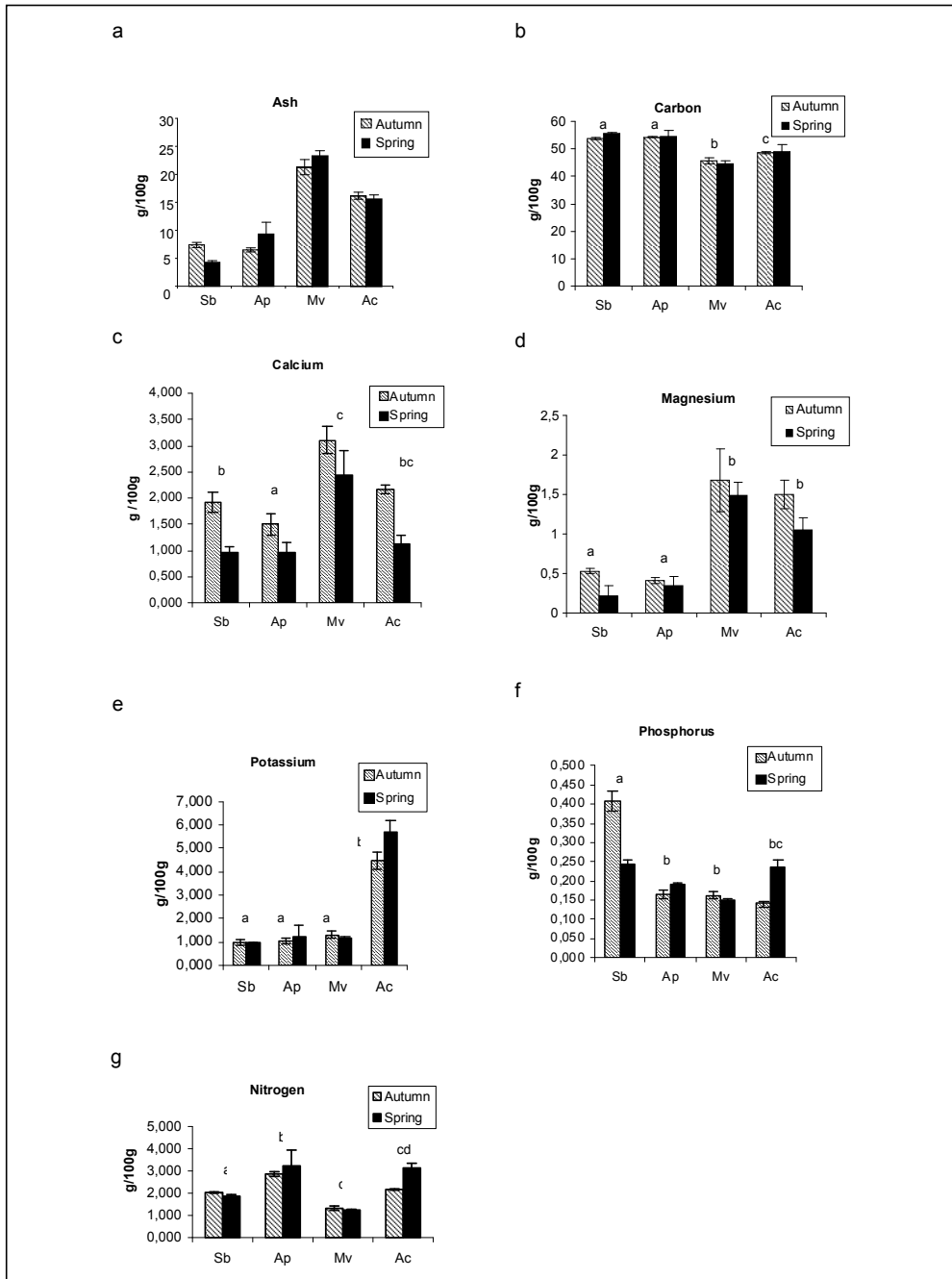


FIG. 2. Contents of elements in the foliar tissues. a. Ash percentage in the foliar tissues. b. Carbon percentage in the foliar tissues. c. Foliar concentration of calcium. d. Foliar concentration of magnesium. e. Foliar concentration of potassium. f. Foliar concentration of phosphorus. g. Foliar concentration of nitrogen.

References: Sb = *Schinopsis balansae*; Ap = *Acacia praecox*; Mv = *Maytenus vitis-idaea*; Ac = *Achatocarpus praecox*.

* Same letters indicate that media are not significantly different at $p < 0.05$ (Student's *t*-test)

TABLE 2. Percentage of leaf fiber and lignin in the foliar tissues.

	Sb	σ	Ap	σ	Ac	σ	Mv	σ
Lignin	6,3	(0,45)	10,43	(2,05)	4,43	(0,70)	7,16	(1,36)
Cellulose	17,16	(0,45)	23,93	(2,80)	10,4	(0,70)	14,76	(1,40)
Hemicellulose	6,4	(1,53)	14,5	(2,45)	26,33	(3,64)	3	(1,73)
Lignin/N	3,32	(5,99)	2,96	(5,46)	1,67	(1,30)	5,59	(2,25)
C/N	28,15	(2,05)	18,12	(1,17)	19,08	(0,59)	35,9	(1,22)
Total N	1,95	(0,14)	3,04	(0,08)	2,65	(0,04)	1,28	(0,09)
NDF	30,06	(1,46)	46,26	(2,75)	42,13	(3,38)	23,2	(0,85)
ADF	23,7	(0,17)	36,63	(10,91)	15,8	(1,70)	22,16	(2,45)

References:

σ = Standard deviation; Sb = *Schinopsis balansae*; Ap = *Acacia praecox*; Ac = *Achatocarpus praecox*; Mv = *Maytenus vitis-idaea*

M. vitis-idaea showed the highest C/N ratio, and one of the two highest litter decomposition rates. *Achatocarpus praecox*, which is third in decreasing order in C/N content (Table 2), also showed a high litter decomposition rate.

Litter decomposition rate. The model fitted accurately to the species studied.

There were significant differences in litter decomposition rates between shrub (*M. vitis-idaea* and *Achatocarpus praecox*) and tree species (*S. balansae* and *Acacia praecox*) ($p < 0.05$). Litter decomposition in shrubs was faster (Fig. 3).

Comparing different segments of the curve (k, decay, and plateau) at microsites with plenty of sunlight we calculated that the k variable presents no significant differences; the biggest differences are in remaining weight (or plateau) and in decay, with 85.75% and 81.35% respectively of total variation.

However, in shaded microsites, decomposition rates (k) show significant differences, with 30.75% of the total variation accounted for by the microsites and 22.65% by the species. Decay values also show significant differences, with 13.28% of the total variation accounted for by species and 3.43% by microsites. No significant differences were found in plateau values.

At microsites with plenty of sunlight, decomposition depends on the species, while in shaded microsites it mostly depends on the microsite itself. According to the calculated decomposition rates, the "half-life" for tree litter accumulation or decay (0.693/k) is two times higher than the "half-life" for

shrub litter, and the time required to reach 95% (3/k) of litter decomposition (Olson 1963) varies according to decomposition rate. In *S. balansae*, with an annual average decomposition rate of -0.04 in the sun and -0.06 in the shade, periods of 75 and 50 years respectively are required. In the case of *Acacia praecox* the period required oscillates between 75 to 100 years, since the decomposition rate varies between -0.04 and -0.03 in the sun and in the shade respectively. *Achatocarpus praecox*, with a decomposition rate between -0.10 and -0.11, requires 27 to 30 years, and *M. vitis-idaea* 20 to 25 years, given average annual values of -0.15 and -0.12 in the sun and in the shade respectively (Carnevale & Lewis 2001).

Relationship between decomposition rate and nutrient, and fiber content. The relationship between decomposition rate and nutrient content was significant and positive for all of the elements (Determination coefficient, $R^2 = 86.33\%$; $p = 0.001$; $b = 0.101$); for Mg ($R^2 = 84.44\%$; $p = 0.001$; $b = 0.107$), for Ca ($R^2 = 57\%$; $p = 0.001$; $b = 0.085$), and for K ($R^2 = 34.34\%$; $p = 0.001$; $b = 0.026$); the relationship was significant and negative for N ($R^2 = 44.53\%$; $p = 0.001$; $b = -0.08$), for P ($R^2 = 14.85\%$; $p = 0.008$; $b = -0.254$), and for total N ($R^2 = 18.84\%$; $p = 0.004$, $b = -0.0448$).

In *Acacia praecox* the relationship between decomposition rate and total N was negative and significant ($R^2 = 18.84\%$; $p = 0.001$), and the value b was -0.08.

In *Achatocarpus praecox* the adjusted correlation coefficient was 10.32 % ($p = 0.02$) for C/N and 15.84% ($p = 0.3$) for lignin/N.

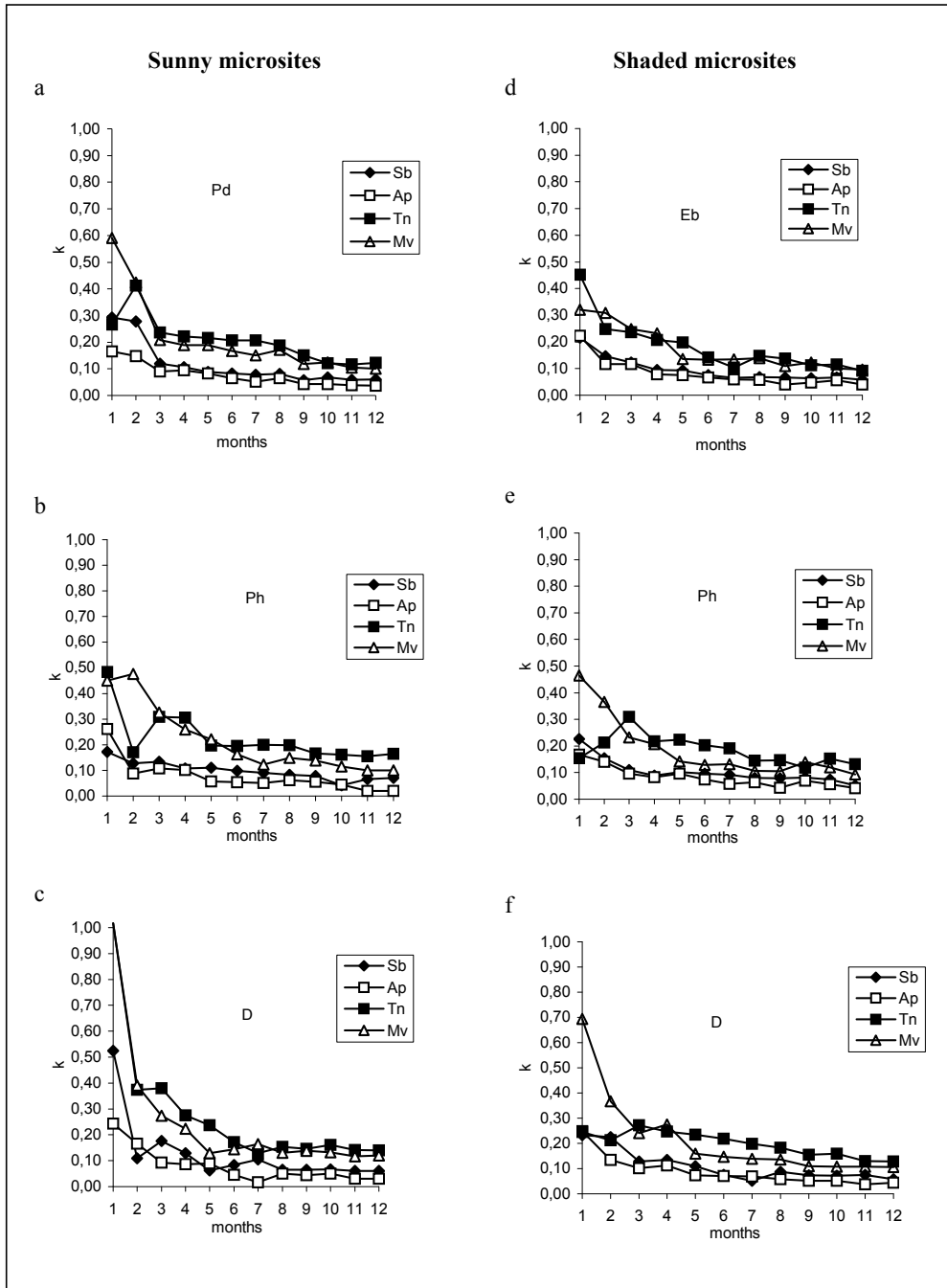


FIG. 3. Litter decomposition rate of four species at the different microsites.

References: Sb = *Schinopsis balansae*; Ap = *Acacia praecox*; Ac = *Achatocarpus praecox*; Mv = *Maytenus vitis-idaea*.

Pd: dry plain; Eb: convex with bromeliads; Ph: humid plain; D: concave.

The relationship between decomposition rate and C/N was significant ($p < 0.05$) although the b value was very low ($b = 0.003$ and $R^2 = 10.32\%$).

The relationship between decomposition rate and lignin and cellulose was negative and significant ($p = 0.001$), although the b values became very low at -0.02 for lignin and -0.007 for cellulose. The relationship between decomposition rate and hemicellulose and lignin/N was not significant.

In the regression analysis, the correlation coefficient was significant and negative for both N and lignin ($p = 0.001$), and the adjustment was moderately strong for both: 45.95%; $b = -0.08$, for the first variable and 43.43%, $b = -0.02$ for the second.

DISCUSSION

Specific leaf morphology variations and litter decomposition rate. Of the four species studied, *Acacia praecox* leaves were the densest, and at the same time they showed the lowest decomposition rate. This could be explained by their higher content of macromolecules such as lignin and hemicellulose. Litter decomposition rate in *Acacia praecox* was lower than in the other species, and inversely proportional to its leaf perimeter/area ratio. This partially contradicts the general assertion that soil microorganisms attack litter with larger perimeter/area ratios faster, thus decomposing litter faster. Foliar volume, or leaf area, showed no influence on decomposition rates.

Leaf nutrient concentration and litter decomposition rate. Species with the highest litter decomposition rates (k) were *M. vitis-idaea* and *Achatocarpus praecox*. They also showed the highest concentration of nutrients in their leaves, Ca and Mg for the former, and Mg and K for the latter.

Higher amounts of Ca and Mg make litter less acidic, making it more palatable and providing an important resource for decomposer organisms (Swift *et al.* 1979, Nicolai 1988, Cornelissen *et al.* 1999). Some decomposer organisms, such as isopods, need high amounts of Ca in their diets for their exoskeleton, while Ca together with Mg, Na, and K are important nutrients for all decomposer organisms (Nicolai 1988).

Calcium is also a significant factor in the decomposition of deciduous species (Berg 1998). In Mexico's tropical rainforest of Los Tuxtlas, litter decomposition rate also seems to be related to leaf nutrient concentrations in woody species (Alvarez-

Sánchez & Becerra Enríquez 1996). In this work, the higher regression values between the decomposition rates and the studied variables corresponded to the sum of elements analyzed, among them Mg and Ca.

Leaf fiber and litter decomposition rate. Generally, litter decomposition rates are inversely related to C/N and lignin/N ratios and positively correlated with nitrogen level. Nitrogen and lignin seem to control litter decomposition in temperate hardwood forests (Melillo *et al.* 1982) as well as elsewhere, such as the Rocky Mountain forests (Stump & Binkley 1992).

In this Chaco Region forest, the highest average of C/N ratio corresponded to *M. vitis-idaea*, which along with *Achatocarpus praecox* showed the highest decomposition rate values, therefore the above assertion did not apply in this case. Data confirm that C/N ratio was not useful in predicting litter decomposition rates, since it takes no account of carbon quality, in other words lignin concentration.

Some authors have stated that lignin concentration is an excellent litter decomposition rate predictor in evenly uniform soils (Cromack 1973, Fogel & Cromack 1977, Entry & Backman 1995, Berg 1998), which is not the case in *S. balansae* forests. However, others have pointed out that litter decomposition rate is inversely correlated with lignin/N ratio (Schelesinger & Hasey 1981, Hobbie 1992). This generalization did not apply to the species analyzed in this paper. *M. vitis-idaea* showed a higher litter decomposition rate than *S. balansae* and *Acacia praecox*. At the same time it showed the highest lignin/N ratio of the four species.

According to several sources, nitrogen concentration is positively correlated with litter decomposition control (Merrill & Cowling 1966, Hobbie 1992), and the same is stated by Upadhyay & Singh (1989) in their analysis of litter decomposition for ten woody species of the Central Himalaya. However, in the *S. balansae* forest, *Acacia praecox* showed the highest nitrogen concentration of the four species studied, and it also showed the lowest litter decomposition rate. This is consistent with Berg (1998), who observes that the lignin loss rate is lower in the nitrogen richest litter and higher in the nitrogen poorest litter. This might be due to the fact that nitrogen lowers lignin decomposition processes. It could explain why low weight molecular nitrogen compounds depress ligninolytic enzyme synthesis in some fungi. Therefore it would be expected that higher foliar nitrogen

concentration might suppress lignin decomposition (Keyser *et al.* 1978). To regulate decomposition rates, lignin-degrading products might react with ammonia or amino acids to form recalcitrant complexes that limit the decomposition rate (Berg 1998). This could explain the lowest lignin loss rate in the richest nitrogen litter.

Schinopsis balansae showed the second lowest litter decomposition rate ($k = -0.06$); this value coincides with the one determined by Prause *et al.* (2003) in Colonia Benítez (Chaco). This species also showed the highest phosphorous concentration. Although the correlation between the decomposition rate and P was relatively weak, these elements might influence their lower decomposition rate, as pointed out by Fogel & Cromack (1977). Alkaloids and phenolic contents in *S. balansae* leaves (Ragonese & Milano 1984, Pelotto & Del Pero 1995) influence the decomposition system (Nicolai 1988). Polyphenols, such as tannins and lignin, have been considered important regulating factors in litter decomposition, as well as in their attraction for herbivorous (Coley *et al.* 1985, Horner *et al.* 1987, Horner *et al.* 1988, Entry & Backman 1995). Perhaps these factors contributed to the remaining weight of *S. balansae* litter being equal to 50% in one year. In this Chaco Region forest, morphological characteristics do not influence the decomposition rate. Shaded microsites have a little influence, and there is no clear relationship between decomposition rates and fiber contents (lignin or the lignin/N rate). The decomposition rate is mainly determined by the nutrients that contribute to litter quality. In the case of *M. vitis-idaea* and *Achatocarpus praecox*, the decomposition rate particularly depends on the Mg and Ca contents. Other research has shown that litter decomposition rate seems to be more related to high leaf nutrient concentration than to microhabitat characteristics (Berg 1998, Upadhyay *et al.* 1989). The humid Chaco Region decomposition rates analyzed in this paper did not follow a common pattern, nor did they correspond to the general models previously mentioned by the authors. While shrubs present a similar decomposition curve, as trees, the causes are different for each of them. Consequently, shrubs with high leaf nutrient concentrations and the highest values of the span in the decomposition curve produced litter that decomposed more rapidly. In the case of the trees, with higher values of the plateau in the decomposition curve, litter decomposition was

limited by high phosphorous concentration in *S. balansae* and nitrogen in *Acacia praecox*. Therefore different decomposition rates make the necessary nutrients available at different periods all year round, providing a balanced supply of nutrients to the whole system. At present the forest is mainly used for cattle raising, and it is regularly cleared of shrubs like *M. vitis-idaea* and *Achatocarpus praecox*, because they are not as profitable as the woody species, and their value as part of the understory is ignored, where they have the potential to increase carbon storage in vegetation and affect soil carbon (Shan *et al.* 2001). From another perspective, these understory shrubs are more than three times faster than trees (*S. balansae* and *Acacia praecox*) at restoring 95% of the nutrients to the system, because of their litter decomposition speed.

CONCLUSION

In these forests, combining salty soils and very dry winters, the consequences of improper management could increase stress conditions for plants. Therefore in any extraction made in the forest, the different nutrient restoration speeds should be considered for each species in order to prevent increasing the instability of the system. One of the strategies of soil carbon sequestration includes the adoption of Recommended Management Practices (RMPs) in forestlands (Lal *et al.* 2003), such as maintenance of the understory that can enhance the soil organic carbon pool (Shan *et al.* 2001). The adoption of restorative land use can reduce the depletion of soil C by soil degradation (Lal 2004), and forest value can be increased if the understory is preserved.

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