Dry weight loss in leaves of dominant species in a successional sequence of the Mesopotamian Espinal (Argentina)

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Abstract

Aim of study: To compare litter decomposition dynamics among different species within a single forest type and also between a single species in different forest successional stages.

Area of study: Different forests of a known successional sequence of the Mesopotamian Espinal, placed in Villaguay Department, Entre Ríos Province, Argentina.

Material and methods: A standard “litter bags” technique was employed. Chemical analyses of C and N were performed for leaves. A regression analysis was applied and data were fitted to a double exponential model. Means estimated among forests and species within each forest were compared using the Tukey-Kramer test.

Main results: The model predicted that leaves would completely mineralize in the mid-term. Leaf decomposition rate in different species (both in the Secondary Forest and Mature forest) had dry matter residues in the following decreasing order: Acacia caven > Prosopis nigra > Prosopis affinis > Celtis ehrenbergiana.

Research highlights: Successional stage was not found to be a factor determining the decomposition rate among species. Different decomposition rates, observed among different species, would not be attributed to initial quality of residues in terms of C and N, but would be associated with a positive feedback process related to nutrient cycle; thus, a greater decomposition would increase nutrient availability and, consequently, litterfall input.

Additional keywords: organic matter; decomposition; litter; dry forest; modeling; plant succession.

Abbreviations used: IF (Initial Forest); MF (Mature Forest); SF (Secondary Forest).

Authors’ contributions: CAM and PGA performed the experiments and wrote the paper with JFGL. MBT and VP analyzed the data.

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Introduction

Decomposition is a biological process whereby litterfall inputs are converted into CO₂ and inorganic compounds. Decomposition of organic residues is a key process in internal nutrient cycling, with a positive return to forest productivity (Gallardo & Merino, 2007).

While degrading processes are associated with leaf aging itself (even when the leaf is still on the tree), the most frequently used method to determine the rate of leaf decomposition has been the use of litter bags, which determines the loss of leaf dry weight (Aceñolaza & Gallardo, 1994; Rovira & Rovira, 2010; Carranza et al., 2012; Bueis et al., 2017). The pattern of leaf litter dry weight generally comprises two phases: an
initial phase, characterized by rapid leaching of soluble compounds and decomposition of labile substances such as sugars, phenols, starches, and proteins; and a second, much slower phase, involving the initiation of degradation of recalcitrant substances such as cellulose, hemicellulose, tannins and lignin (Arellano et al., 2004).

Decomposition of leaf litter deposited on the floor of natural forests or of forests subjected to silvopastoral use implies the incorporation of nutrients to the soil that is relevant for sustainability of those ecosystems (Prause et al., 2012). Decomposition of leaf litter inputs makes nutrients available to the plant community (Carranza et al., 2012). Nutrient flux can be slowed down, with key chemical elements for forest productivity being transiently retained in some of the different compartments (aerial biomass, litter and soil organic carbon; Gallardo & González, 2004).

The Argentine Espinal is a forest ecosystem located between 28º and 40º S, to the south of the Chaco Ecoregion, with an estimated total area of 33,000,000 ha (Lewis et al., 2006); it forms a large arch that surrounds the Pampas grassland to the west. This ecosystem is dominant in an extensive area of the South American Southern Cone and is subjected to silvopastoral use.

The Mesopotamian Espinal (Entre Ríos, Argentina) includes the forests of Espinal Phytogeographic Province, Ñandubay District (Cabrera, 1976). In several areas of Entre Ríos, an intensive modification of the Mesopotamian Espinal is observed in the rural landscape due to the advance of the agricultural frontier, which has produced an important reduction of the forest area (Arturi, 2006) accompanied with an increasing heterogeneity pattern (Aceñolaza, 2000). As a consequence, primary forests have been transformed, generating a successional sequence characterized by secondary forests that are degraded by forest exploitation for timber production (focused on the logging of Prosopis nigra), subsequent inappropriate livestock management, or as a consequence of excessive firewood extraction (affecting the species Acacia caven and Prosopis affinis).

After deforestation and abandonment of croplands, an initial successional stage (IF) is established, dominated by a woodland of A. caven; subsequently, this secondary formation (SF) is colonized by P. affinis, which may be defined as an intermediate stage; finally, the mature forest stage (MF) is reached, with the appearance and dominance of P. nigra, thereby the primary forest is reestablished (Mendoza et al., 2012).

To determine the sustainability of silvopastoral systems in the Mesopotamian Espinal, it is important to characterize the dynamics of leaf decomposition of the tree typical species that compose the successional sequence of these forests, since such decomposition regulates nutrient return to the soil and, therefore, largely conditions its fertility.

The aims of this work were to: a) determine the process of weight loss via leaf decomposition, by fitting a regression model; b) determine if a single species has different decomposition dynamics according to the forest successional stage; and c) compare decomposition dynamics among different species within a single forest type.

**Material and methods**

**Study area**

The study area is in the province of Entre Ríos, Argentina, between 31º 47’ 59” S and 59º 11’ 38” W. Within this area, three experimental plots were selected and studied, each belonging to one of the stages of the successional sequence (Fig. 1): IF, SF and MF. IF is a monospecific forest of Acacia caven (Molina) Molina; this area had been a cropland that was abandoned in 1998 and later naturally colonized by this species. SF is dominated by Prosopis affinis Spreng, and presents other typical species, such as A. caven and Celtis ehrenbergiana (Klotzsch) Liebm.; some of the trees are up to 50 years old. MF is the reestablished primary forest dominated by P. nigra (Griseb.) Hieron., with the presence of A. caven, P. affinis, and C. ehrenbergiana; some trees of the dominant species are more than 80 years old.

These three forest formations presented a production of litter of 1.14, 2.95, and 2.91 Mg DM/ha·yr, (DM: dry matter) respectively; they have been evaluated by Mendoza et al. (2012) who showed the real heterogeneity of the landscape, with a floristic richness represented by species of the family Fabaceae (A. caven, P. affinis, and P. nigra) that possess biological binding capacity of the atmospheric N₂; they are potentially important in terms of the transfer of N to the soil in processes of decomposition, and only C. ehrenbergiana (without the ability to biologically fix the atmospheric N₂) belonging to the family Celtidaceae, would not have this potentiality (Mendoza et al., 2014).

**Characterization of climate, soil of the study area**

The climate in the study area is temperate-humid; mean annual precipitation is above 1000 mm/yr, with important interannual variation (INTA, 2000). Rainfall occurs throughout the year, with notable increases in autumn and spring. Mean annual temperature is 16 ºC,
with the mean of the coldest and hottest months being 11 °C (July) and 25 °C (January), respectively.

Climatic data shown in Fig. 2 correspond to the period when the decomposition assay was performed. Those data points were obtained from the automatic meteorological station of the Bolsa de Cereales, located near the study area (http://centrales.bolsacer.org.ar/pluviometros/).

Soils were formed during the Quaternary from the deposition of sediments corresponding to Hernandarias Formation (Aceñolaza, 2007). Those materials were of palustrine-lacustrine origin and originated soils with high contents of expanding clays (montmorillonite). These soils are, therefore, of clay texture, deep, with poor drainage, with calcareous concretions from -90 cm in depth downwards, and scarce in available P. Taxonomically, soils in the area correspond to the order Vertisol, with slightly acid pH (6.3 ±0.7) and, in general, with high soil organic matter (SOM) content of 5.4 ±3.0%, depending on land use intensity (INTA, 2000).

Method used for the study of dry weight loss from leaf decomposition

The study was conducted using the litterbags standard technique (Aceñolaza & Gallardo, 1994; Carranza et al., 2012). The bags were 18 x 15 cm² in size, and made of 100-μm mesh; this mesh size was selected because the tested species have very small follicles.

Leaves were collected in autumn (May 2010) from the crown of four trees per species and forest type, using pruning shears as proposed by León et al. (2009). The leaves were dried in an 80 °C heater (Dalvo Sb343, Argentine) until constant weight was obtained. Then, 3.00 g of leaf of each species were weighed and placed in litter bags. The leaves of the different species were not mixed; the experimental design consisted by placing litterbags in the different forests, as follows: IF (32 litter bags of A. caven), SF (32 litter bags of A. caven, 32 of P. affinis, and 32 of C. ehrenbergiana), and in MF (32 litter bags of A. caven, 32 of P. affinis, 32 of...
C. ehrenbergiana, and 32 of P. nigra). Litter bags were placed on the floor under canopies of trees, according to the species studied in the successional sequence, simulating conditions of natural decomposition. Later, litterbags were randomly removed (four bags per forest and per species) between May 2010 and May 2012, at: 7, 20, 40, 80, 160, 300, 500, and 700 days since the start of the assay. The leaf litter was taken to the laboratory, dried in an 80°C heater until constant weight was reached, and weighed with an electronic balance (T-Scale, NHB-600, Taiwan).

**Chemical analyses of leaves**

Chemical analyses of C and N were performed, and the C/N ratio was calculated for leaves, per species and forest, taken from samples of leaf litter fell during the 2009-2010 period. A sample from each season, year and species was analyzed.

All samples were dried in an 80 °C heater and then ground with a ball mill (Retsch, MM301, Germany).

Chemical analyses were then performed to determine C content (total Carbon, mg C/g dry matter) using dry combustion (Wösthoff, Carmhograph12, Germany), and N content (total nitrogen, mg N/gDM) using a segmented flow auto-analyzer (Bran+LuebbeAA3, Germany).

**Statistical analyses**

A regression analysis was applied, considering residual dry matter as dependent variable and time as independent variable (Jenny et al., 1949; Olson, 1963; Rovira & Rovira, 2010).

Data were fitted to a double exponential model (Bunel & Tait, 1974) plus a constant, following the Eq. [1]:

$$\frac{X_t}{X_0} = ae^{-(k_1 t)} + be^{-(k_2 t)} + c$$  \[[1]\]

where $$X_0$$ = initial amount of leaf litter (g DM); $$X_t$$ = amount of remaining material (g) after a time period $$t$$; $$a$$ = mass of the fraction of fast decomposition rate in (g/g); $$b$$ = mass of the fraction of slow decomposition rate (g/g); $$c$$ = asymptote that quantified the recalcitrant fraction; $$k_1$$ = decomposition rate of the fast fraction (yr$$^{-1}$$); $$k_2$$ = decomposition rate of the slow fraction (yr$$^{-1}$$); $$t$$ = time (yr) spanned between $$X_0$$ and $$X_t$$. The restriction $$a + b + c = 1.0$$ was also considered.

With the parameters ($$a, b, c, k_1,$$ and $$k_2$$) obtained in each of the non-linear regressions, the values of dry matter weight loss ($$X_t/X_0$$ in g DM/g) for the 8-time periods used in the model (7, 20, 40, 80, 160, 300, 500, and 700 days) were estimated.

For each of the parameters calculated, an analysis of variance was performed with two inter-individual factors, using a hierarchical design (forest and species nested within forest) using the Eq. [2]:

$$y_{jk(i)} = \mu + \alpha_i + \beta_j(i) + \epsilon_{jk(i)}$$  \[[2]\]

where $$y_{jk(i)}$$ = value estimated for parameter $$y$$ in the sample $$k$$ of the species $$j$$ in the forest $$i$$; $$\mu$$ = general mean effect; $$\alpha_i$$ = principal effect of forest $$i$$; $$\beta_j$$ = principal effect of species $$j$$ within forest $$i$$; $$\epsilon_{jk(i)}$$ = random error for the value estimated of $$y$$ in sample $$k$$ of species $$j$$ within forest $$i$$, with $$\epsilon_{jk(i)} \sim N(0, \sigma^2)$$, where $$\sigma^2$$ is random variance of the model.

The different values of $$\alpha_i$$, $$\beta_j$$ and $$\epsilon_{jk(i)}$$ were: $$i = 1, 2, 3$$ for initial, secondary and mature forests, respectively; $$j = 1$$ (species A. caven) if $$i = 1$$; $$j = 1, 2, 3$$ for the species A. caven, P. affinis and C. ehrenbergiana, respectively, if $$i = 2$$; and $$j = 1, 2, 3, 4$$ for the species A. caven, P. affinis, C. ehrenbergiana and P. nigra, respectively, if $$i = 3$$; and $$k = 1, 2, 3, 4$$ for the replications of each species within each forest.

Finally, the means estimated among forests and species within each forest were compared using the Tukey-Kramer test with a significance level of 0.05. Normality of residuals was compared using the Kolmogorov-Smirnov test, and homogeneity of variances, via the Levene test, using SAS 9.2 statistical package (SAS Inst., 2005).

The values corresponding to dry matter for each collection time (0, 7, 20, 40, 80, 160, 300, 500, and 700 days) were compared using a mixed linear model analysis of variance (McCulloch & Searle,2001) with two inter-subject factors employing a hierarchical design (forest and species nested within forest).

Mean concentrations of C, N and C/N were compared using a mixed linear model analysis of variance (McCulloch & Searle,2001) considering two inter-subject factors employing a hierarchical design (forest and species nested within forest).

**Results**

**Analysis of the loss of dry weight in leaves of the tree species of the Mesopotamian Espinal: fit of the model**

The results showed high values of coefficients of determination ($$r^2$$) in the fit of Eq. [1] (Table 1), which ranged between 95.1% and 99.3%. This model predicts that the leaves of all the species evaluated will be completely mineralized in the mid-term (a few years), since parameter $$c$$ (which would correspond to recalcitrant material with a too long decomposition time)
tended statistically to zero in the studied species (Table 1), whereas parameters \( a, b, k_1 \) and \( k_2 \) were statistically different from zero.

**Temporal patterns of leaf dry weight loss in species present in different forests**

The comparison of the parameters obtained in the decomposition model, for a single species in different forests, showed that for *A. caven* (species present in the three forests of the successional sequence) parameter \( a \) reaches an average value of 16% of the initial weight, without significant differences among forests. Decomposition constant \( (k_1) \) of fraction \( L \) did show significant differences, with significantly higher values in \( SF \) (94.6/yr) than in \( IF \) and \( MF \), which had values of about 50/yr (without significant differences between \( IF \) and \( MF \); Table 1). This \( L \) fraction of rapid decomposition had half-life times (ln2/ \( k_1 \)) for *A. caven* of 2.7, 4.9, and 5.3 days, for \( SF, IF, \) and \( MF \), respectively, indicating that half of this fraction was lost in less than a week. Fraction \( b \) did not show significant differences among forests, with \( R \) being about 84% of the initial amount (and, therefore, the dominant fraction); decomposition constant \( (k_2) \) of \( R \) did not show significant differences among forests for this species, with values close to 0.70/yr; and the calculated half-life time of this fraction (ln2/ \( k_2 \)) was approximately one year (Table 1).

Regarding *P. affinis* (a species common to both \( SF \) and \( MF \) forests), the comparison of coefficient \( a \) did not show significant differences between forests, with \( L \) fraction representing about one third in both forests. Decomposition constant \( k_1 \) of \( L \) did not show significant differences between forests, with values close to 30/yr (also corresponding to a half-life of about 8.4 days). Coefficient \( b \) did not also show significant differences between forests, with fraction \( R \) being close to 68%; similarly, constant \( k_2 \) did not show significant differences between \( SF \) and \( MF \), with values close to 0.80/yr (Table 1).

Parameters \( a, b, k_1, \) and \( k_2 \) corresponding to *C. ehrenbergiana* (species common in \( SF \) and \( MF \)) did not also show significant differences between forests, as observed for *P. affinis* (Table 1).

Figures 3, 4a and 4b, show the temporal evolution of weight loss in the three forests for the species *A. caven, P. affinis* and *C. ehrenbergiana*, respectively.

*Acacia caven* (present in \( IF, SF \) and \( MF \)) and *P. affinis* (present in \( SF \) and \( MF \)) showed no significant differences in residual dry weight values (which were 22 and 15%, respectively; Figs. 3 and 4a) after 700 days of decomposition. Likewise, they showed similar temporal evolution of weight loss between those forests, since there were no significant differences between them in any of the compared sampling dates.

In contrast, *C. ehrenbergiana* showed significant differences in residual dry weight values at the end of the assay, with 9 and 11% in \( SF \) and \( MF \), respectively (Fig. 4b); their temporal evolutions were similar up to 80 days of decomposition; after that sampling date, the recorded weight loss values were significantly higher in \( SF \) than in \( MF \) (Fig. 4b).

**Temporal patterns of leaf weight loss of different species within each type of forest**

The comparison of parameters among species within a single forest showed significant differences both in

| Table 1. Mean values (including ± standard error) of the parameters obtained by applying the double exponential model (Equation 1) and results of ANOVA by species and forest. | Forest | Species | n | \( A \) (g/g) | \( b \) (g/g) | \( c \) (g/g) | \( k_1 \) (y\(^{-1}\)) | \( k_2 \) (y\(^{-1}\)) | \( r^2 \) (%) |
|---|---|---|---|---|---|---|---|---|---|
| IF | *A. caven* | 4 | 0.15 (±0.06) a | 0.85 (±0.06) a | 0 | 52.2 (±15.5) b | 0.68 (±0.08) a | 95.1-97.8 |
| SF | *A. caven* | 4 | 0.18 (±0.06) Ba | 0.82 (±0.06) Aa | 0 | 94.6 (±15.5) Aa | 0.68 (±0.08) Ba | 96.3-97.1 |
| | *P. affinis* | 4 | 0.30 (±0.06) Aa | 0.70 (±0.06) ABa | 0 | 32.1 (±15.5) Ba | 0.82 (±0.08) Ba | 98.3-99.1 |
| | *C. ehrenbergiana* | 4 | 0.40 (±0.06) Aa | 0.60 (±0.06) Ba | 0 | 11.8 (±15.5) Ba | 1.03 (±0.08) Aa | 97.2-99.3 |
| MF | *A. caven* | 4 | 0.15 (±0.06) Ba | 0.85 (±0.06) Aa | 0 | 48.1 (±15.5) Ab | 0.70 (±0.08) Ba | 95.1-97.4 |
| | *P. affinis* | 4 | 0.33 (±0.06) Aa | 0.67 (±0.06) Ba | 0 | 24.5 (±15.5) Aa | 0.75 (±0.08) Ba | 96.5-98.1 |
| | *C. ehrenbergiana* | 4 | 0.28 (±0.06) Aa | 0.72 (±0.06) Ba | 0 | 32.9 (±15.5) Aa | 0.98 (±0.08) Aa | 96.3-97.5 |
| | *P. nigra* | 4 | 0.29 (±0.06) A | 0.71 (±0.06) B | 0 | 19.0 (±15.5) A | 0.73 (±0.08) B | 95.6-98.5 |

*IF*: initial forest, *SF*: secondary forest, and *MF*: mature forest. Different uppercase letters indicate statistically significant differences among different species within a single forest type, and different lowercase letters indicate statistically significant differences between shared species in different forests (Tukey-Kramer test, \( p<0.05 \)). Significance levels for the effects “forest” and “species (forest)”: ***\( (p <0.001) \); **\( (p <0.01) \); *\( (p <0.05) \) and ns “non-significant”. |
SF and MF (Table 1). Leaves of *C. ehrenbergiana* showed a significantly higher decomposition constant \(k_2\) of R fraction in both forests (SF and MF) than the constants of the three-leguminous species. Furthermore, leaves of *A. caven* in SF had significantly different values for parameters of L fraction (lower in \(a\) and higher values \(k_1\)) from those of the other two species present; in MF the same significant differences were observed for parameter \(a\), but not for \(k_1\).

Table 2 shows the leaf contents of C, N and the C/N ratio. The high values recorded in the leguminous species agree with the expected values.

Figures 5 and 6 show the temporal evolution of leaf dry matter, expressed as a proportion, for *A. caven*, *P. affinis*, *C. ehrenbergiana*, and *P. nigra* in secondary (SF) and mature (MF) forests, respectively. Rates of weight loss were compared only among different species of SF and MF, since only one species was present in IF. In general, percentage of remaining dry matter at the end of the assay in the species of the Mesopotamian Espinal ranged between 22% in *A. caven* and 10% in *C. ehrenbergiana* (Figs. 5 and 6).

In SF, significant differences in temporal evolution of the three species were observed. As shown in Fig. 5, a higher loss of labile substances was recorded at the start of the decomposition process (7, 20, and 40 days) in *P. affinis* and *C. ehrenbergiana* than in *A. caven*; after 80 days and until the end of the assay, the three species differed significantly, with *A. caven* and *C. ehrenbergiana* being the species with the lowest and highest decomposition rates, respectively.
Table 2. Contents of C and N, and C/N ratio of leaves at the start of the decomposition assay (standard error is indicated in parentheses).

| Forest | Species          | n | C (mg/g dry matter) | N (mg/g dry matter) | C/N   |
|--------|------------------|---|---------------------|---------------------|-------|
| IF     | A. caven         | 8 | 495 (±21)           | 24.5 (±3.5)         | 20.2 (3.2) |
| SF     | A. caven         | 8 | 481 (±32)           | 27.2 (±3.1)         | 18.8 (4.5) |
|        | P. affinis       | 8 | 492 (±26)           | 29.2 (±3.2)         | 18.0 (3.9) |
| MF     | A. caven         | 8 | 486 (±45)           | 24.8 (±7.0)         | 19.6 (2.9) |
|        | C. ehrenbergiana | 8 | 492 (±26)           | 29.2 (±3.2)         | 18.0 (3.9) |
| MF     | P. affinis       | 8 | 496 (±42)           | 28.4 (±3.4)         | 17.5 (4.9) |
|        | C. ehrenbergiana | 8 | 480 (±56)           | 26.2 (±5.8)         | 18.3 (3.8) |
|        | P. nigra         | 8 | 497 (±51)           | 28.3 (±5.4)         | 18.3 (4.2) |

Effect

| “forest” | “species(forest)” |
|-----------|-------------------|
| ns | ns | ns |

IF: initial forest, SF: secondary forest, and MF: mature forest. Forests were compared using the Tukey-Kramer test (p<0.05) for the effects “forest” and “species (forest)”; ns: non-significant.

**Secondary forest**

![Figure 5](image)

**Figure 5.** Temporal evolution of dry matter (DM) of leaves, referred as a proportion of 1.00 g DM of *Acacia caven* (Ac), *Prosopis affinis* (Pa), and *Celtis ehrenbergiana* (Ce) in the secondary forest (SF). Different lowercase letters indicate significant differences (p<0.05) between species for each date.

**Mature forest**

![Figure 6](image)

**Figure 6.** Temporal evolution of dry matter (DM) of leaves, referred as a proportion of 1.00 g DM of *Acacia caven* (Ac), *Prosopis affinis* (Pa), *Celtis ehrenbergiana* (Ce), and *Prosopis nigra* (Pn) in the mature forest (MF). Different lowercase letters indicate significant differences (p<0.05) between species for each date.
Decomposition rate in MF did not show significant differences among the four species (A. caven, P. affinis, C. ehrenbergiana, and P. nigra) at the start of the assay (7 days). Between 40 and 160 days, however, A. caven differed significantly from the other three species. In addition, C. ehrenbergiana and P. nigra did not show significant differences between them (Fig. 6).

From day 300 and up to the end of the assay, the species with the lowest and highest decomposition rates were A. caven and C. ehrenbergiana, respectively, with significant differences from each other and from the other two Prosopis species (P. affinis and P. nigra). The last two species exhibited intermediate decomposition dynamics, with no significant differences between them on the different sampling dates of this study (Fig. 6).

Discussion

Dry weight loss in leaves of the tree species from the Mesopotamian Espinal

The model applied here (Bunnel & Tait, 1974) differs from those typically proposed in the specialized literature (Jenny et al., 1949; Olson, 1963; Aceñolaza & Gallardo, 1994; León et al., 2011) as it present the parameter c (corresponding to a highly recalcitrant fraction). This parameter predicts that, leaves of all the evaluated species, will mineralize in the short- to mid-term, since all the species yielded values close to zero (Table 1). While term a correspond to the very labile fraction (L) that will decompose according to constant k₁, term b corresponds to the relatively resistant material (R) that decomposes according to constant k₂.

Total leaf decomposition might explain, among other aspects, the productive sustainability of these forests given by the effects of nutrient return via leaf litter. Previous studies conducted by Mendoza et al. (2014) in the same study area showed that N and P are abundant elements in litterfall of these species; hence, an efficient recycling would allow soil fertility to be maintained (or even increased).

The rapid and complete decomposition in the Mesopotamian Espinal can be attributed to the low C/N ratio in leaves at the start of the assay, without significant differences among species (Table 2) as well as to the good soil moisture levels and optimum temperature values suitable for the development of microorganisms almost throughout the annual cycle (Rojas & Saluso, 1987). According to Aceñolaza & Gallardo (1994) and León et al. (2011), low C/N is a factor associated with a high leaf litter decomposition rate, besides the favorable climatic conditions of moderate temperatures and a short period of water deficit, which are characteristic in our study area.

Our results are somewhat different from findings of Carranza et al. (2012) for the Argentine Arid Chaco (involving different species), who recorded lower decomposition constants. The different behaviors between the Arid Chaco and the Mesopotamian Espinal may be attributed not only to the different C/N ratios but also to the presence of a marked annual period of water deficit in the Arid Chaco, which influences decomposition rate of the residual organic matter (Fioretto et al., 2005). As these forests are not fertilized to promote herbaceous species production, it is important to conserve the diversity and density of N-fixing woody native species to ensure productivity of the silvopastoral system; Carranza et al. (2012) found that the presence of trees in selective clearings promotes nitrogen release from native pastures.

The comparison of the parameters among species within a single forest type (Table 1) showed that A. caven had the lowest coefficient a values, corresponding to the L fraction, with significant differences from the remaining species (both in SF and in MF), indicating a higher number of recalcitrant substances in A. caven leaves than in leaves of the other species. Therefore, the leaves of P. affinis, C. ehrenbergiana, and P. nigra may lose greater labile substances through leaching (water-soluble substances) than in A. caven; Aceñolaza & Gallardo (1994) and Prause et al. (2002, 2012) confirmed the occurrence of rapid labile and water-soluble substances leaching in species of subtropical forests used for silvopastoral activities.

By contrast, A. caven had the highest term b, which corresponds to fraction R, both in SF and in MF. This result indicates a greater presence of slowly-decomposing substances in these leaves.

Interestingly, C. ehrenbergiana (Family Celtidaceae) had significantly higher decomposition constant (k₁) values of fraction R (both in SF and MF), suggesting a higher decomposition rate than that of the other species of the family Fabaceae. This result cannot be attributed to the leaf C/N ratio, since their values were statistically similar; Table 2). The fact that the non-leguminous species (C. ehrenbergiana) did not show significant differences from the other species indicates that it is a nutrient-demanding species (i.e., it needs a high amount of available nutrients in soils). This characteristic of C. ehrenbergiana explains its presence in the succession only after the secondary forest has established (taking advantage of the N abundance through nitrogen fixation by the previously established leguminous species, especially A. caven).

Therefore, it may be attributed to the nature of organic substances (lower tannin and lignin content; Arellano et al., 2004; Goma-Tchimbakala & Bernhard-Reversat, 2006), which has not been evaluated in this work and should be considered in future works.
Temporal patterns of leaf weight loss

In general, the initial phases of decomposition were rapid in the forests of the Mesopotamian Espinal, as evidenced by the high $k$ values, possibly due to the abundance of precipitation and relatively high summer temperature (Fig. 2) favoring lixiviation and microbial activity. This phenomenon was confirmed by Castellanos & León (2011) in a study of leaf litter decomposition in Acacia mangium plantations. By contrast, weight loss in the Argentine Arid Chaco is characterized by an initial slow phase followed by a rapid phase (Torres et al., 2005), with an opposite pattern in the rate of each decomposition phase, which was related to the local climatic conditions and the chemical composition of the materials.

The comparison of different species between SF and MF systems (Figs. 4b and 5) showed significant differences in the residues remaining at the end of the assay, following a decreasing order: $A. caven > P. nigra > P. affinis > C. ehrenbergiana$.

It has been reported that a faster decomposition rate involves a faster nutrient movement (Gallardo & González, 2004). Accordingly, of all the studied species, C. ehrenbergiana had the most active biogeochemical cycle associated with demanding species at intermediate to stable successional stages. This phenomenon might be indicating a match between decomposition rates and nutritional demands associated with productivity and litterfall contribution according to the species; if decomposition had been slow, available nutrients might have been insufficient, which would have limited plant growth and development, as reported by Montagnini & Jordán (2002) and, therefore, litterfall input.

The greatest litterfall inputs of C. ehrenbergiana were associated with a higher productivity and decomposition rate of the produced litterfall (Mendoza et al., 2012), as opposed to the lower litterfall input of A. caven which, in turn, had a lower decomposition rate. Prause et al. (2002) observed that in Argentine Chaco forests, Schinopsis balansae Engl. was the species that most largely contributed litterfall to the soil (although it had a lower decomposition constant), compared with litterfall inputs of P. nigra; therefore, this system seems to be have differently from the Mesopotamian Espinal.

Conclusions

We found significant differences, in leaf decomposition rates, between tree species that compose the forest (both in SF and MF); the remaining organic residues had, in general, the following decreasing order: $A. caven > P. nigra > P. affinis > C. ehrenbergiana$.

Considering the factors influencing litterfall decomposition processes, we conclude that the different decomposition rates observed among species are not attributable to the initial quality (C and N) of litter. The successional stage of the forests is not a factor determining decomposition rate of the most frequent species at different stages in the Mesopotamian Espinal. C. ehrenbergiana litter promotes a rapid decomposition in this native forest, confirming its importance for biodiversity conservation of both woody plants and native grasses, and pasture sustainability.

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